



THE BRITISH RHAETIC FLORA



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BRITISH MUSEUM
(NATURAL HISTORY) *k*

THE BRITISH RHAETIC FLORA

BY

THOMAS MAXWELL HARRIS *Xref*
PROFESSOR OF BOTANY IN THE UNIVERSITY OF READING

WITH FIVE PLATES AND TWENTY-SIX FIGURES
IN THE TEXT

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PREFACE

ALTHOUGH extensive floras of approximately Rhaetic age are known from many parts of the world, only few and fragmentary plant remains have yet been found in the British Rhaetic rocks. Professor T. M. Harris, however, whose minute and detailed examination of the Rhaetic Flora of Greenland has opened up new fields in Mesozoic palaeobotany, has succeeded, by the application of modern methods of investigation, in revealing the presence in these beds of an extremely interesting micro-flora. In addition, he has discovered many fresh details of structure in the small plant *Naiadita*, which has been known for nearly a century, though its true botanical position has only now become apparent. On the basis of these new facts Professor Harris has further examined current theories of the morphology and phylogeny of the Bryophyta. The Trustees of the British Museum are fortunate in having secured the services of Professor Harris for this work.

W. D. LANG
Keeper of Geology

March 1938

AUTHOR'S PREFACE

THE flora of the British Rhaetic was described by Seward (1904) in Part II of his Catalogue of the Jurassic Flora. A new account has become necessary because a certain horizon has now provided an unsuspected flora of a novel type; the rest of the British Rhaetic is very poor in plants and those that occur are but scattered and rather miserable specimens. The discoveries made in the *Naiadita* Bed suggest that the micro-fossils of other horizons of the Rhaetic might well repay close study, though the softness of most of the rock (which easily breaks down to mud) would make such a study troublesome. All the specimens described here belong to hard beds of limestone or sandstone which occur at intervals among the soft shales.

The main collections of British Rhaetic plants were made during last century. Since then a few specimens only have been preserved as samples for stratigraphic purposes, as it was imagined that the material had little to show of botanical interest. Recently, however, now that its value has been realised, a good deal of fresh material has been collected.

The considerable majority of the specimens dealt with in this Catalogue are included in the British Museum collection, and I am indebted to the Keeper of the Geological Department for permitting me to study them. For the sake of completeness I have also described and in some cases figured specimens belonging to other collections: the Geological Survey and Museum, the Municipal Museum and Art Gallery of Bristol, and the Geological Museum of Reading University. I am most grateful to the Directors of these museums and to Dr. R. Crookall of the Survey, Dr. F. S. Wallis of Bristol, and Professor H. L. Hawkins of Reading for lending me these specimens.

I would also like to thank Mr. L. A. Richardson for help with stratigraphy, Mr. W. E. Nicholson and Professor W. H. Lang for providing material of recent Bryophytes for comparison, and Mr. G. A. Kellaway for helping me in the field and providing many specimens of his own collecting. Finally, I would like to thank Mr. W. N. Edwards and Mr. F. M. Wonnacott for their help in forwarding this work.

T. M. HARRIS



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PRESENTED
13 JUN 1938

INTRODUCTION

THE Rhaetic Flora consists of two distinct parts: the flora of the *Naiadita* Bed, and the remaining flora. The former consists of very small plants associated with aquatic animals, and is, I think, the flora of shallow freshwater lakes preserved *in situ* or near where it grew. This flora is well preserved and unique.

The other flora consists of fragments of comparatively large land plants very much worn and perhaps deposited far from their position of growth. In so far as they are determinable they are species of wide distribution. There is nothing in any way exceptional about this flora, and because it is poor it has little scientific interest.

STRATIGRAPHY

The main Rhaetic outcrop stretches across England from Dorset to North Yorkshire, and there are smaller outcrops in Wales, North Ireland and Scotland, but it is from England alone that plants have been obtained. In its maximum development, the Rhaetic series consists of about a hundred feet of rock, most of which is barren, but with a number of horizons with fossil animals. Nearly all these animals are marine, and the British Rhaetic is regarded as largely marine, but it has a peculiar facies. The chief fossils are fish and small lamellibranchs; there are no ammonites. For this reason its correlation with the typical marine Rhaetic of the Alps is imperfect; moreover, the zones of the Alpine Rhaetic are not well known (Spath 1934).

The base of the marine beds, in most places, that is, the oldest shales containing *Pteria contorta*, is taken as the beginning of the Rhaetic, but in a few places there are some older marine rocks (Sully Beds) which may also be included. The position assigned to the upper boundary has varied somewhat; it is usually taken to be at the top of the Langport Beds and below the *subplanorbis* Beds, both of which are marine and contain a few distinct lamellibranchs but no ammonites. Thus, although usually recognisable in England, neither the beginning nor end of the English Rhaetic are such as can be closely correlated with the Alpine Rhaetic.

A more satisfactory level in the Rhaetic itself is provided by the lamellibranchs, particularly *Pteria contorta*. This is nearly always common where shells occur at all in the lower or Westbury Series, but is never found in the upper or Cotham Series. *Pteria contorta* is widespread in Europe, and in the Alps is found only in the older zones with the ammonite *Choristoceras haeri*.

Those who have studied the Rhaetic differ in the way they treat it. Some have regarded it as a stage of the Keuper, some as a stage of the Lias (since it is the beginning of the Liassic submergence), others avoid this difficulty by regarding it as a mere passage series or else as a separate formation. The enormous thickness of marine Rhaetic rock in the Alps suggests that it represents a considerable period, too long, in fact, to be dismissed as a passage series. The British Rhaetic, which is never more than about a hundred feet thick and is often less, may represent no more than a few fragments or episodes of the whole period. A recently expressed view (Spath 1934) is that the Rhaetic is best regarded as the last stage of the Trias, its ammonites being more like those characteristic of the upper Trias than those of the lower Lias. From the point of view of stratigraphy in Britain, Arkell (1933) finds it most convenient to include it with the Jurassic, and the same might be said for its fossil plants, though I think this is due merely to our poor knowledge of the floras of the preceding stages of the Triassic.

Partly because of its fragmentary nature, and also because it has been very closely studied, the British Rhaetic has been divided into a considerable number of stages which are persistent and recognisable with certainty over a good many miles, though perhaps not outside this country. Such a stage is the *Naiadita* Bed, which is clearly recognisable over a considerable area. A stratigraphic table of the English Rhaetic, taken from Richardson's works, is given below.

Lower Lias—Pre-*planorbis* Beds, 0–20 ft.

Upper Rhaetic	{	Watchet Beds, 0–8 ft.	{	<i>Pseudomonotis fallax</i> — "Cotham marble" Ostracod Beds <i>Estheria</i> and <i>Naiadita</i> Beds Ostracod Beds	
		Langport Beds or White Lias			0–25 ft.
		Cotham Beds, 0–19 ft.			

Lower Rhaetic	{	Westbury Beds. Various layers—up to 47 ft., with <i>Pteria contorta</i> (Portlock)
		Sully Beds, 0–14 ft.

Upper Keuper—Tea green marls.

N.B.—Some geologists place the Liasso-Rhaetic boundary rather lower, but all include the Cotham Beds in the Rhaetic.

There is no record of any plant other than a piece of lignite from the older Rhaetic (with *Pteria contorta*), though this is

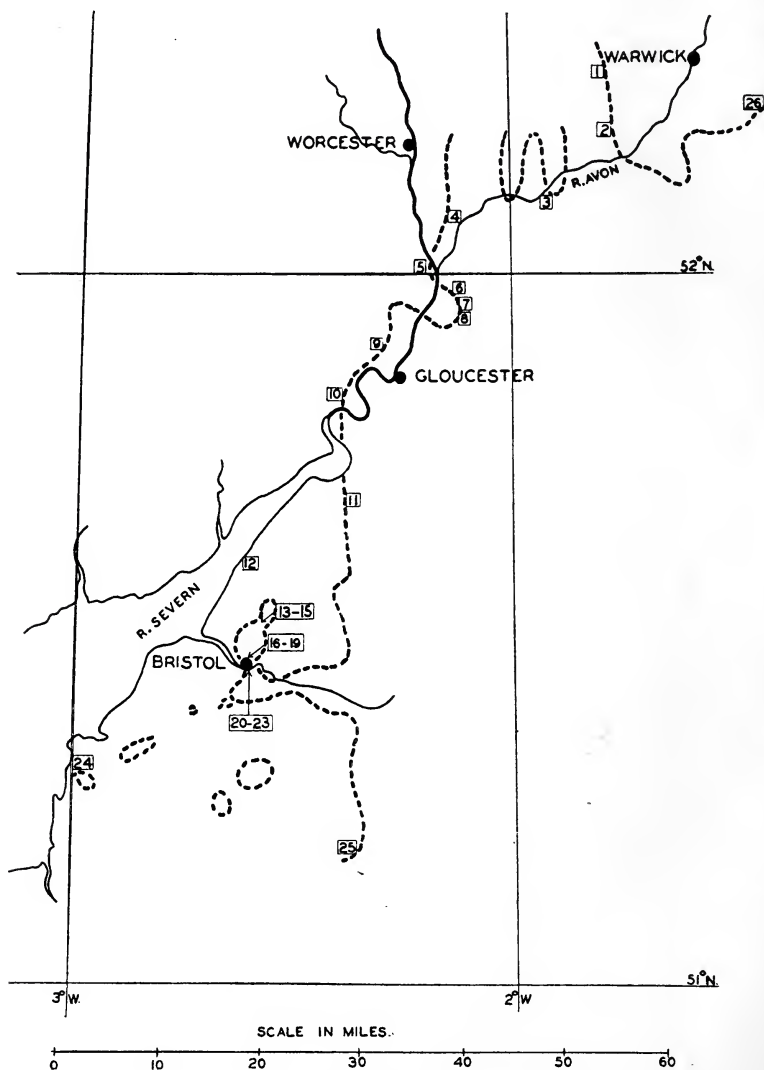
almost certainly the age of rich plant beds in various parts of Europe. The plants occur in the younger Rhaetic (Cotham series) either in its lower part—the *Naiadita* bed—or in its upper part in beds doubtfully separated from the Lias; they may, in fact, be Liassic.

The *Naiadita* bed which contains the main flora is a thin but remarkably constant bed which is found over about half of the English Rhaetic outcrop. It extends from just to the east of the Mendip Hills in Somerset to south Worcestershire and Warwickshire, a distance of ninety miles (Text-fig. 1). In this area it is known from a great many sections, in fact from nearly all which have been described in detail. It is remarkable that such an insignificant fossil as *Naiadita*—in its usual disintegrated state—should have been so much noticed, but it marks a definite horizon of stratigraphic value. It is absent from the south (Dorset), from the west (Somerset west of the Mendip Hills and S. Wales) and the north (Leicestershire, Nottinghamshire). Sometimes the absence of *Naiadita* has been commented on by the author describing the section, but even where it is not mentioned it may be presumed that it was looked for and that no *Naiadita* bed is present, or at least none with macroscopic remains.

The *Naiadita* bed itself is by no means uniform, but usually has many thin layers of different character. No details of this have been published, and I am in no position to do so as the material I collected had been thrown out of position. In one of the best Bristol localities (Redland, see Short 1904) the greater part of the rock is described as barren, but there are numerous layers in which *Naiadita* is abundant, and interbedded with some of these are layers rich in fish teeth, scales and marine shells. Much the same is evidently true of the neighbouring locality I visited. I may add that the plant material varies, often being represented by large specimens in one layer, and by minute fragments in the next. The character of the bed varies in much the same way from place to place, though the rock is always calcareous. Some of the associated plants and animals are remarkably constant, but there is variation in their relative abundance.

Short (1904) has pointed out that the three chief types of fossil of the *Naiadita* bed—*Naiadita*, fish remains, and the crustacean *Estheria*—tend to avoid one another's company; this is also true of some of the rocks I have examined, though in certain localities *Estheria* and *Naiadita* are associated. Prolonged search through the *Naiadita* layers does, it is true, yield an occasional tooth or *Estheria*, and I found a tetrad of *Naiadita* spores and a rhizoid in a fish layer, but never large specimens of the plant. Still another facies has been noticed, though only in a few places; this is a sun-cracked layer (Kellaway & Oakley 1934), or a sun-cracked layer with ripple marks and worm tracks (Short 1904),

which indicate either drying or else very shallow water. It is significant that no old land surface penetrated by roots occurs anywhere.



TEXT-FIG. I

Sketch map of part of the Rhaetic outcrop (shown by a thick broken line). The numbers refer to the localities given below.

1. Three localities in the North of Arden, Warwickshire:—Umberslade, Mows Hill, South of Tanworth (Matley 1912).

2. Five localities in the South and East of Arden:—Shrewley, Rowington, Shelfield (Horwood 1909, Matley 1912), Wootton Wawen (Brodie 1865); Stoopers Wood (Richardson 1912).
3. Woodnorton, Evesham. (Richardson 1903a, 1904c); Cracombe—see p. 64.
4. Bourne Bank, Defford (Richardson 1903).
5. Brockerbridge Common, Bushley (Richardson 1903); Upton-on-Severn, a few miles north of Bushley—see p. 64.
6. Gray Hill, Apperley (Richardson 1903).
7. Coombe Hill (Richardson 1903).
8. Wainlode Cliff (Richardson 1903).
9. Near Minsterworth (Richardson 1903).
10. Garden Cliff, Westbury-on-Severn (Richardson 1903).
11. Standhill Green, Stinchcombe, Gloucester (Richardson 1904a).
12. Aust (Short 1904, Tutchter 1930).
13. Filton (Tutchter 1909).
14. Charlton (Tutchter 1909).
15. Stoke Gifford (Short 1904, Reynolds & Vaughan 1904).
16. Coldharbour Farm, Redland, New Clifton, Bristol (Several sections). (Parsons 1899, Wickes 1901, Short 1904).
17. Cotham Road, Bristol (Short 1904).
18. Henleaze Road, Bristol (Kellaway 1937).
19. Southmead Laundry, Westbury, Bristol. Specimen collected by Wickes—see p. 65.
20. Pylle Hill, Bristol (Wilson 1891, 1894).
21. West Town Lane, Brislington, Bristol (Kellaway 1935).
22. Crox Bottom, Novers, Bristol. Specimens collected by Kellaway—see p. 64.
23. Bedminster, Bristol. Specimens in collection of Geol. Survey and Museum—see p. 64.
24. Uphill, Nr. Weston-super-Mare—2 sections (Richardson 1911, Kellaway & Oakley 1934).
25. Vallis Vale, Near Frome—2 sections (Richardson 1911).
26. Harbury Cutting, S.-W. of Warwick—see p. 64.

The following picture is suggested (see p. 51). The Rhaetic sea which transgressed the Triassic desert was, as is well known, shallow and dotted with islands. Slight changes of level would readily isolate considerable areas, and this apparently happened repeatedly during the formation of the *Naiadita* bed. Under a moderately wet climate these lagoons would soon become brackish or fresh-water lakes; *Naiadita* then formed a pure growth over the bottom under the shallow water, and was preserved wherever sedimentation was occurring, the sediment being partly silt but largely very fine calcium carbonate, formed as a precipitate. Temporary incursions of the sea would end the life of *Naiadita* and its associates and give a fish bed, and this would be followed by regression of the sea and re-establishment of fresh-water life. The few fish teeth in the *Naiadita* layers might represent derived fossils, and the same might be true of the occasional spores in the fish layers.

The following animals are found associated with *Naiadita* (i.e. are characteristic of the plant-filled layers):

<i>Darwinula liassica</i> (Brodie)	} abundant
<i>Darwinula liassica</i> var. <i>major</i> Jones	

Estheria minuta in certain localities

A large insect larva called a dragon-fly nymph by Wickes (rare)

A very small insect larva with a slender body and large eyes (this is very common but has not previously been recorded)

A small oval fossil like an egg—abundant

Certain other minute fossils of problematic nature

(Species more characteristic of the fish layers are excluded.)

The fauna of the fish-bearing layers is very much larger, but no separate lists have been made, the following being recorded for the bed as a whole. The author given in brackets is the one who has most recently recorded the species.

PISCES:

<i>Acrodus minimus</i> Ag.	(Short 1904)
<i>Gyrolepis albertii</i> Ag.	(Short 1904, Kellaway 1935)
<i>Hybodus minor</i> Ag.	(Short 1904)
<i>Saurichthys acuminatus</i> Ag.	(Short 1904)
<i>Pholidophorus</i> sp.	(Wickes 1901)
<i>Lepidotus</i> sp.	(Wickes 1901)
<i>Legnonotus</i> sp.	(Wickes 1901)
Coprolites	(Short 1904)

MOLLUSCA:

<i>Isocyprina ewaldi</i> (Bornemann)	(Short 1904)
<i>Isocyprina depressa</i> (Moore)	(Short 1904)
<i>Protocardia rhaetica</i> (Merian)	(Kellaway & Oakley 1934)
<i>Protocardia philippiana</i> (Dunker)	(Tutcher 1909)
<i>Dimyopsis intusstriata</i> (Emmrich)	(Wilson 1891)
<i>Chlamys valoniensis</i> (Defr.)	(Kellaway 1935)
<i>Cardita</i> (<i>Palaeocardita</i>) <i>cloacina</i> (Quenstd.)	(Tutcher, 1909)
<i>Cardinia regularis</i> Terquem	(Short 1904)
<i>Modiolus minimus</i> (J. Sowerby)	(Short 1904)
<i>Pleuromya</i> sp.	(Short 1904)
<i>Actaeonina</i> sp.	(Wilson 1891)
<i>Pteromya crowcombeia</i> Moore	(Short 1904)

CRUSTACEA:

<i>Estheria minuta</i> v. <i>brodieiana</i> Jones	(Tutcher 1909, 1930)
<i>Darwinula liassica</i> (Brodie)	(Kellaway 1935)

INSECTA:

"Beetle elytra and wings"	(Short 1904)
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[The list of molluscs has been kindly revised by Dr. L. R. Cox.]

TECHNIQUE

The fossils of the *Naiadita* bed are preserved in a somewhat peculiar way which makes necessary some modification of the usual methods for investigation. They are preserved in a hard, very fine-grained matrix consisting largely of calcium carbonate. The organic material of the cell walls is present and its fine details are very clearly shown, but as a rule it has lost its strength and can only be detached from the rock in minute fragments. Often, too, the plane of cleavage lies in the specimen, patches of the compressed material adhering to both sides.

In certain layers the plant remains are merely flattened to form "compressions," but more commonly there is a certain amount of calcite in the cells and there is always a good deal of matrix between neighbouring organs such as leaves, so that the specimen is by no means reduced to one plane, but is in a state intermediate between a typical "compression" and a typical "petrification."

For investigation ordinary thin rock sections were tried, but the method was not suitable. The method of obtaining sections by celloidin pulls (following etching with hydrochloric acid) and celloidin and balsam transfers proved useful for certain purposes, though the rottenness of most of the cell walls once they are cleared of the rock matrix limits the use of such methods. For most purposes these methods are unnecessary; the fine details are clearly seen when the specimen is immersed in oil and observed by light from above. When dry, on the other hand, scarcely anything can be seen, and I think that the reason why previous workers overlooked much of the structure of *Naiadita* was that they examined the material dry. After a good deal of experiment I have found that oils are better than water, alcohol or glycerine; and of these oils two proved most useful—xylol and paraffin. I used xylol where it was desirable to have the specimen dry again in a minute or two, but for most purposes where this was undesirable or immaterial I used paraffin. This was the ordinary commercial burning oil, "kerosene" (boiling point about 150° to 200° C.), roughly purified by the addition of a little bromine and then shaking with sodium hydroxide. Besides cheapness, this liquid has the advantages of rather slow but ultimately complete evaporation, and absence of smell and poisonous qualities.

Where a specimen was appreciably calcified, or where there was much matrix between overlying organs, methods of serial sections gave valuable results. Two ways were tried—carefully controlled etching, and scraping away the rock with a needle. The needle method proved much the more precise, for with practice it is possible to scrape out 5 μ or even less of rock from a single cell. The matrix is slightly transparent, and this is a great help.

This method of surface dissection in paraffin oil under the microscope might perhaps be applied with advantage to other small calcareous petrifications.

Other methods which gave valuable results were maceration of the rock in bulk—first in hydrochloric acid to disintegrate it and remove calcium carbonate, then in hydrofluoric acid to remove silica. This yields spores and the alga *Botryococcus*; the other fossils are too weak to withstand this treatment. Preparations of the spores exposed on the rock surface can be made very quickly by scraping them off and clearing them with hydrochloric acid; no other treatment is necessary.

It may be mentioned in passing that a few specimens were preserved rather differently, the lumen of the cell being more or less filled up with little concretions of ferric oxide.

A certain number of the specimens, which had become very grimy in the course of many years' preservation in museums, needed cleaning before the plants could be seen, and by experiment a suitable method was found. The rock is covered with a thin solution of cellulose nitrate in alcohol and ether; on drying, the film peels off removing all the dirt, but without removing any of the fossil material.

THE COLLECTIONS

In the systematic part of the Catalogue, the provenance of the specimens in the Geological Department of the British Museum (Natural History) is indicated in abbreviated form:

P. B. Brodie Coll. . . .	Rev. P. B. Brodie Collection, part presented, 1886; remainder purchased, 1895.
G. A. Kellaway Coll. . .	Presented by Mr. G. A. Kellaway, 1936.
G. A. Kellaway & T. M. Harris Coll. . .	Presented by Mr. G. A. Kellaway and Professor T. M. Harris, 1937.
W. McPherson Coll. . .	Presented by Mr. W. McPherson, 1903.
L. Richardson Coll. . .	Purchased, 1914.
T. J. Slatter Coll. . .	Purchased, 1896.
J. W. Tutcher Coll. . .	Presented by Mr. J. W. Tutcher, 1904.
W. H. Wickes Coll. . .	Presented by Mr. W. H. Wickes, 1900, 1928.

SYSTEMATIC DESCRIPTIONS

SECTION I.—THE FLORA OF THE *NAIADITA* BED

THALLOPHYTA

ALGAE

Genus **BOTRYOCOCCUS** Kützing, 1849, p. 892

Botryococcus braunii Kützing

(Text-fig. 2)

- 1849 *Botryococcus braunii* Kützing, p. 892.
1892 *Reinschia australis* Bertrand, C. E., p. 465. (*Nomen nudum*).
1892 *Pila bibractensis* Bertrand, C. E., p. 479, pl. xiii A, figs. 1-16; xiii B, figs. 21-23.
1892 *Pila bibractensis* Bertrand, C. E.: Bertrand, C. E. & Renault, pp. 216, 219.
1892a *Pila bibractensis* Bertrand, C. E.: Bertrand, C. E. & Renault, p. 159, pl. vi; vii, figs. 22, 23.
1893 *Pila*: Bertrand, C. E. & Renault, pp. 512-48, pl. xxiii, figs. 1-10 bis.
1893 *Pila minor* Bertrand, C. E., & Renault, pp. 541-3.
1893 *Pila bibractensis* Bertrand, C. E.: Bertrand, C. E., & Renault, pp., 541-2.
1893a *Reinschia australis* Bertrand, C. E., & Renault, p. 321, pls. iv-vii.
1893b *Reinschia australis* Bertr. & Ren.: Bertrand, C. E., & Renault, p. 490.
1893c *Pila bibractensis* Bertrand, C. E.: Bertrand, C. E., & Renault, p. 595.
1893c *Reinschia australis* Bertr. & Ren.: Bertrand, C. E., & Renault, p. 595.
1894 *Pila bibractensis* Bertrand, C. E.: Bertrand, C. E., p. 64, pl. v, figs. 18-22.
1894 *Reinschia australis* Bertr. & Ren.: Bertrand, C. E., & Renault, photos 1-28.
1894 *Reinschia australis* Bertr. & Ren.: Bertrand, C. E., p. 64, pl. v, figs. 23, 24.
1896 *Reinschia australis* Bertr. & Ren.: Bertrand, C. E., p. 193.
1896 *Pila bibractensis* Bertrand, C. E.: Renault, p. 514, text-figs. 131-4, pls. A, B, atlas pl. lxxxviii, figs. 2-4, 10.
1896 *Pila karpinskyi* Renault, p. 552.
1896 *Pila minor* Bertr. & Ren.: Renault, pp. 536-7, text-fig. 136.
1896 *Pila scotica* Renault, p. 544, text-figs. 140-143.
1896 *Reinschia australis* Bertr. & Ren.: Renault, p. 540, text-figs. 137-9.
1896 *Thylax britannicus* Renault, p. 549, text-figs. 144, 145.
1898 *Epipolaiu boweri* Bertrand, C. E., p. 179, pl. xi, figs. 119-24.
1898 *Botryococcites largae* Bertrand, C. E., p. 182, pl. xi, figs. 127-32.
1899 *Pila liasica* Renault, p. 985, pl. xviii, figs. 9-18.
1899 *Pila bibractensis* Bertrand, C. E.: Renault, p. 991, pl. xix, figs. 1-17; text-figs. 12-17.
1899 *Pila karpinskyi* Ren.: Renault, p. 1037, pl. xxi, fig. 7.
1899 *Pila kentuckyana* Renault, p. 1032, pl. xxiii, fig. 4.
1899 *Pila scotica* Ren.: Renault, p. 1022, pl. xxi, figs. 13-16; p. 1060, text-fig. 22; p. 1075.

- 1899 *Reinschia australis* Bertr. & Ren.: Renault p. 1010, pl. xx, figs., 1-6 text-figs. 18, 19.
- 1899 *Reinschia capensis* Renault, p. 1018, pl. xx, figs. 7-12.
- 1899 *Thylax britannicus* Ren.: Renault, p. 1028, pl. xxi, figs. 1, 2.
- 1899 *Pila lusitanica* Renault, p. 1075, pl. xxii, fig. 17.
- 1900 *Pila bibractensis* Bertrand, C. E.: Renault, pp. 8, 9.
- 1900 *Pila minor* Bertr. & Ren.: Renault, pp. 8, 9.
- 1901 *Reinschia australis* Bertr. & Ren.: Bertrand, C. E., p. 639.
- 1914 *Pila bibractensis* Bertrand, C. E.: Zalessky, pp. 496, 503.
- 1914 *Botryococcus braunii* Kütz.: Zalessky, pp. 497, 503.
- 1917 *Gloeocapsomorpha prisca* Zalessky, p. 36, pl. ii, figs. 4-7; iii, figs. 1, 2.
- 1917a *Gloeocapsomorpha prisca* Zal.: Zalessky, p. 374.
- 1917a *Pila* sp.: Zalessky, pp. 376-9.
- 1925 *Elaeophyton coorongiana* Thiessen, p. 126, pls. xxvii-xxxi, xxxviii B-xl.
- 1925 *Reinschia australis* Bertr. & Ren.: Thiessen, p. 131, pls. xxxii, xxxiii, xxxiv A.
- 1925 *Pila scotica* Ren.: Thiessen, p. 132 pls. xxxiv B, xxxv-xxxviii A.
- 1926 *Botryococcus braunii* Kütz.: Zalessky, p. 35, pl. xi, fig. 6; xii, figs. 1-3, 5.
- 1926 *Pila karpinskyi* Ren.: Zalessky, pp. 31, 42, pl. xii, fig. 4.
- 1926 *Pila kentuckyana* Ren.: Zalessky, pp. 31, 42, pl. xii, figs. 6, 7.
- 1927 *Botryococcus*: Bertrand, P., p. 695.
- 1927 *Botryococcus*: Pia in Hirmer, pp. 56, 693.
- 1927 *Pila karpinskyi* Ren.: Pia in Hirmer, p. 56.
- 1927 *Pila kentuckyana* Ren.: Pia in Hirmer, p. 56.
- 1927 *Pila bibractensis* Bertrand, C. E.: Pia in Hirmer, p. 56.
- 1927 *Pila liasica* Ren.: Pia in Hirmer, p. 56.
- 1927 *Reinschia australis* Bertr. & Ren.: Pia in Hirmer, p. 56, text-fig. 34.
- 1927 *Gloeocapsomorpha prisca* Zal.: Pia in Hirmer, p. 35, text-fig. 19.
- 1927 *Thylax britannicus* Ren.: Pia in Hirmer, p. 57.
- 1930 *Pila bibractensis* Bertrand, C. E.: Bertrand P., p. 161, pls. i-iv, text-figs. 1, 3.
- 1930 *Botryococcus braunii* Kütz.: Bertrand, P., p. 162, text-figs. 6-11.
- 1930 *Reinschia australis* Bertr. & Ren.: Bertrand P., p. 163, pls. v-vii, text-figs. 12-17, 19.
- 1936 *Botryococcus braunii* Kütz.: Blackburn in Blackburn & Temperley, p. 841, pl. i, figs. 1-7, text-figs. 1-4.
- 1936 *Botryococcus braunii* Kütz.: Temperley in Blackburn & Temperley, p. 858, text-figs. 1, 2.
- 1936 *Pila*: Temperley in Blackburn & Temperley, p. 855, etc., pl. i, figs. 8-10; ii, figs. 11-14, 23.
- 1936 *Reinschia*: Temperley in Blackburn & Temperley, p. 855 etc., pl. ii; text-figs. 13, 15-22, 24.
- 1937 *Botryococcus braunii* Kütz.: Harris in Kellaway, p. 226.

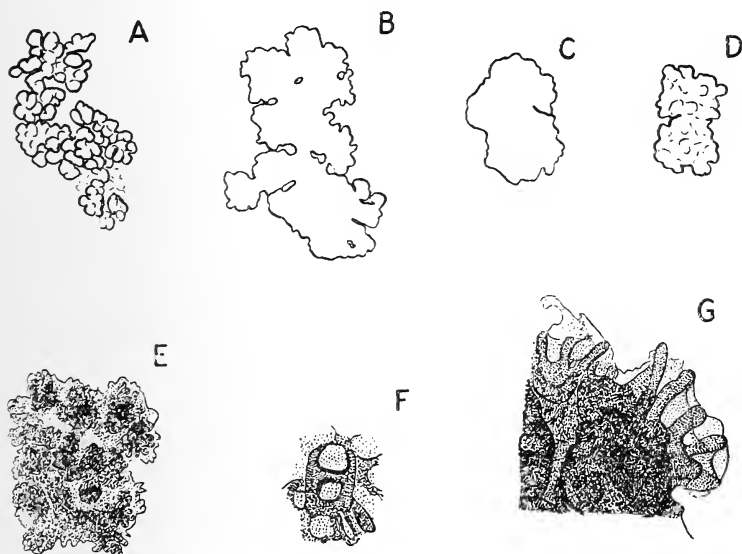
HORIZON.—*Naiadita* Bed, Upper Rhaetic.

LOCALITIES.—Whole extent of Bed, but especially Henleaze Road, Bristol.

DESCRIPTION.—Specimens agreeing very closely indeed with other fossil material of *Botryococcus* are abundant in the *Naiadita* bed of certain localities. The colonies form very conspicuous little masses of a bright terra-cotta colour (varying from pinkish to deep orange-red). They can be readily dug out of the matrix and cleaned with acid, since the parts of the colony are united tenaciously. The material composing the colony is remarkably resistant: it is only very slowly bleached by $\text{HNO}_3 + \text{KClO}_3$, and

after long treatment with this reagent still withstands dilute alkali; it is in fact the most resistant fossil in the bed.

The general appearance of typical colonies is shown in Text-fig. 2; a large proportion of the colonies are elaborately branched like these. In searching for material of *Botryococcus* it was sometimes found difficult to discriminate without chemical methods between them and little ferric oxide concretions, though the ferric oxide is usually a darker red. These little spheres of ferric oxide are by no means easy to dissolve in $\text{HNO}_3 + \text{KClO}_3$,



TEXT-FIG. 2. *Botryococcus braunii*.

A, large colony as seen on rock surface, V. 25297, $\times 60$. B, another colony after removal from the rock, slide V. 25299, $\times 60$. C, D, smaller colonies isolated from the rock, slide V. 25298, $\times 60$. E, part of a small colony at a higher magnification, slide V. 25298, $\times 160$. F, part of the surface of a colony showing a pair of capsules, slide V. 25298, $\times 700$. G, margin of colony showing a number of capsules, slide V. 25298, $\times 700$.

but at no stage of solution do they show the transparency or the cup-like structure of *Botryococcus*. They can be easily dissolved by a warm mixture of hydrochloric and oxalic acids, which does not affect the *Botryococcus* colonies.

DISCUSSION.—The use of the name of a living alga, *Botryococcus braunii* Kützing, for an ancient fossil (dating apparently from the Ordovician) raises a question of nomenclature of some importance. The specimens agree very perfectly with the living alga, but with no other organism; on the other hand, they cannot show all the features which can be demonstrated in fresh material.

Two possible courses which are open are:

- (a) To use the same name, as is done here.
- (b) To use a different name or names for some or all of the fossils.

The reason why the same name has been used is that all the organisms in question are considered to be morphologically identical. This principle has long been accepted by palaeontologists, many of whose genera, and even species, identified with living forms have a long range in the past.

The usage of palaeobotanists varies. Those working with younger Tertiary and Quaternary plants use names of living genera and species freely; some of those working with older Tertiary and with Mesozoic plants do so; others use new generic names (often distinguished by the suffix *-ites*). Few occasions to use a generic name of a recent plant arise in the Palaeozoic.

The weight to be given to the reasonable doubt whether an imperfectly known fossil is identical with a living genus (or species) must ultimately be a personal matter. There appears, for example, to be a difference in the value of the evidence that the fossil *B. braunii* is identical with the living form, and that *Stenixys* is identical with *Cosmarium*; though the identity of *Stenixys* might be reconsidered if the pitting of a placoderm desmid could be demonstrated in it. To frame rigid rules of procedure for the use of these names seems hopeless, but at the same time it is clear that no difference of age can by itself be used as a valid distinction for a genus or species.

In the above synonymy I have only included a few relevant references to the recent alga; the list of names given to the fossil forms, though doubtless incomplete, is fairly comprehensive. Blackburn and Temperley's recent paper (1936), which not only describes fully the living *Botryococcus braunii*, but summarises the different views on its variously named fossil representatives, renders it unnecessary for me to discuss the subject in detail. Further references to papers on the boghead controversy may be found in this paper, and in Thiessen (1925) and P. Bertrand (1930).

A tribute may be paid to the perspicuity of Edgeworth David, who in 1889 not only recognised the resemblance of "*Reinschia*" to algae such as the Volvocaceae, but also suggested a comparison between the Australian boghead and "coorongite" many years before the discovery that the latter was due to the living *Botryococcus braunii*. C. E. Bertrand too deserves credit for noting, in a paper which has been generally overlooked, the resemblance between *Botryococcus braunii* and his *Botryococcites largae*, which he further compared with *Pila*, *Reinschia* and *Epipolaia* (1898, pp. 181, 183).

The geological distribution of this extremely persistent alga may be summarised as follows under the original names, now all regarded as synonyms of *Botryococcus braunii*:

ORDOVICIAN: *Gloeocapsomorpha prisca* (Esthonia).

CARBONIFEROUS: *Pila karpinskyi* (Russia), *P. kentuckyana* (U.S.A.), *P. scotica*, *Epipolaia boweri*, *Thylax britannicus* (Scotland), *P. lusitana* (Spain).

PERMIAN: *Pila bibractensis*, *P. minor* (France), *Reinschia australis* (N. S. Wales), *R. capensis* (S. Africa).

RHAETIC: *Botryococcus braunii* (England).

JURASSIC: *Pila liasica* (Hungary), *Pila* sp. (Russia).

OLIGOCENE: *Botryococcites largae* (France).

PLEISTOCENE: *Botryococcus braunii* (Europe).

RECENT: *Botryococcus braunii* (world-wide), *Elaeophyton coorongiana*.

Botryococcus is present on nearly every large hand-specimen, and no attempt has been made to catalogue it fully. The following list merely represents the localities from which it has been obtained. It has not been observed in material from the following localities—Bourne Bank, Defford; Pyllle Hill, Totterdown, Bristol; Bedminster, Bristol. However, in none of these was the material adequate for a proper search and its apparent absence is not significant.

- V. 25297. Text-fig. 2 A. Henleaze Road, Bristol. *Kellaway and Harris Coll.*, 1937. (This alga is present on the majority of specimens from this locality.)
- V. 25298. Slide. Text-fig. 2 C-G. Henleaze Road, Bristol. *Kellaway and Harris Coll.*, 1937.
- V. 25299. Slide. Text-fig. 2 B. Henleaze Road, Bristol. *Kellaway and Harris Coll.*, 1937.
- V. 3397. A typical colony. Also slide V. 3397a. (Also catalogued under *Naiadita*.) Wainlode Cliff, Gloucester. *P.B. Brodie Coll.*, 1895.
- V. 4015. Block a. A typical colony. (Also catalogued under *Naiadita*.) Redland, Bristol. *W. H. Wickes Coll.*, 1900.
- V. 13170. Well-preserved colonies. (Also catalogued under *Naiadita*.) Also slide V. 13170a. Coombe Hill, Cheltenham, Gloucester. *L. Richardson Coll.*, 1914.
- V. 13172. A typical colony. (Also catalogued under *Naiadita*.) Lane Cutting, 3/10 mile S. of Highgrove, Nr. Minsterworth, Gloucester. *L. Richardson Coll.*, 1914.
- V. 13174. Well-preserved colonies. (Also catalogued under *Naiadita*.) Also slide V. 13174a. Garden Cliff, Westbury-on-Severn, Gloucester. *L. Richardson Coll.*, 1914.
- V. 13175. A fairly well preserved colony. (Also catalogued under *Naiadita*.) Also slide V. 13175a. Hapsford Mills, The Vallis, Nr. Frome, Somerset. *L. Richardson Coll.*, 1914.
- V. 24809. A typical colony. (Also catalogued under *Naiadita* and *Hepaticites*.) Pen Park Road, Southmead, Bristol. *G. A. Kellaway Coll.*, 1936.
- V. 24811. A typical colony. (Also catalogued under *Naiadita* and *Branched Filaments*.) Uphill Road cutting, Weston-super-Mare. *G. A. Kellaway Coll.*, 1936.

Collection of the Geological Survey and Museum:

- 56513. Well-preserved colonies. (Also catalogued under *Naiadita* and *Stenixys*.) Crox Bottom, Novers, Bristol. Presented by G. A. Kellaway, 1937.

Collection of the Bristol Municipal Museum and Art Gallery:

Cb. 2663. Occasional colonies. (Also catalogued under *Naiadita* and Branched Filaments.) Southmead Laundry, Westbury, Bristol.

Genus **STENIXYS** nov.

1937 *Stenixys* (*nomen nudum*) Harris in Kellaway, p. 226.

DIAGNOSIS.—Minute body consisting of two similar "semicells" connected by an "isthmus." End view of semicells oval.

Stenixys bears a close resemblance in size and shape to the very common type of desmid represented by *Cosmarium* and its allies. I have little doubt, whatever its real nature, that its wall at least has the same general shape as in *Cosmarium*, because certain specimens are full of calcite or ferric oxide and, having escaped much compression, show their form clearly. I would on available evidence classify *Stenixys* as a desmid. The high degree of uniformity shown by the different individuals accords with this view, but I have not been able to obtain any confirmatory evidence from the structure of the wall. The wall is compact and strong enough to be detached as pieces up to 50μ square, and readily yields celloidin pulls after careful etching. It reacts in a similar way to the cell walls of *Naiadita*, being unaffected by HCl or cold concentrated H_2SO_4 , but charred and disintegrated by hot H_2SO_4 , and rather quickly bleached and oxidised by $HNO_3 + KClO_3$ in the cold, after which it is dissolved by alkali. I examined the wall carefully to find traces of pitting, but found none. When dry it appears polished, with irregularities due to preservation; when mounted in water, glycerine or balsam it appears homogeneous under a low magnification, and a magnification of about 1,000 is needed to show the unevenness which even then is indistinct and irregular. The significance of this should not, however, be over-emphasised, as the pitting of even large placoderm desmids is often fine and might be unrecognisable in a fossil.

Another fact which may perhaps be judged to militate against the suggestion that *Stenixys* is a desmid is that all but one of the individuals examined are complete—having both semicells. In many recent desmids the semicells come apart after death.

If *Stenixys* is correctly assigned to the desmids it is of considerable botanical interest, as this group is scarcely known from any but the most recent deposits.

Ehrenberg, who in 1834 instituted the genus *Xanthidium* for certain recent desmids, subsequently referred to this genus, in two cases actually to living species, some spherical spiny bodies from Cretaceous flints, and also from supposed brackish-water boulders of uncertain age (1837, 1838, 1854). Some at least of these fossils, however, being marine, are more likely to be eggs of some invertebrate, as Pia (1927, p. 55) and other authors have

remarked. None of them has yet been confirmed as an authentic desmid. C. E. Bertrand (1898, p. 73, pl. ii, figs. 48a, b) figured a "desmidiform body" which was fairly common in the Oligocene bituminous schist of Bois d'Asson (Basses-Alpes), but though he noted its resemblance to *Cosmarium* he refrained from referring it definitely to the desmids. The inadequate figures do not suffice for any further expression of opinion.

The name is from στενός, narrow, and ἱστός, a waist.

***Stenixys cosmarioides* sp. n.**

(Pl. V, fig. 4; Text-fig. 3)

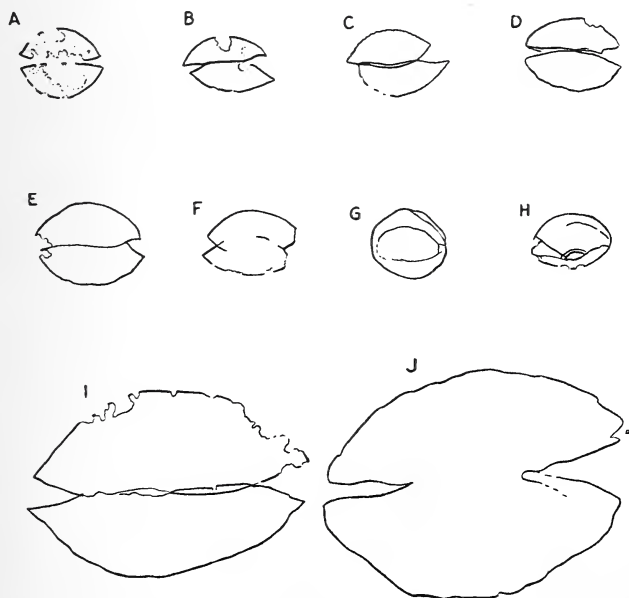
1937 *Stenixys cosmarioides* (*nomen nudum*) Harris in Kellaway, p. 226.

DIAGNOSIS.—Length of complete organism, 190 μ ; width of each semicell, 250 μ . Surface smooth, but basal angles of semicell acutely pointed.

HOLOTYPE.—V.25308 (Text-fig. 3 J).

HORIZON.—*Naiadita* Bed; Upper Rhaetic.

LOCALITIES.—Bristol district.



TEXT-FIG. 3. *Stenixys cosmarioides*.

A-H, $\times 45$

A, V. 25300; B, V. 25301; C, V. 25302; D, V. 25303;
E, V. 24810a; F, V. 25304; G, V. 25305; H, V. 25306.

I, J, $\times 140$.

I, V. 25307; J, Type-specimen, V. 25308.

Stenixys is easy to recognise (after immersion in oil) as its wall is a characteristic blackish-brown colour, appreciably different from the lighter brown of the walls of *Naiadita*. It must be counted an uncommon member of the flora—in all only twenty-four specimens were recognised; many of these, being very imperfect, were sacrificed in an attempt to make out the wall structure.

- V. 25300, Text-fig. 3 A; V. 25301, Text-fig. 3 B; V. 25302, Text-fig. 3 C; V. 25303, Text-fig. 3 D; V. 25304, Text-fig. 3 F; V. 25305, Text-fig. 3 G; V. 25306, Text-fig. 3 H; V. 25307, Text-fig. 3 I; V. 25308, type-specimen (Text-fig. 3 J); all from Henleaze Road, Bristol. *Kellaway and Harris Coll.*, 1937.
 V. 24810a. (Text-fig. 3 E). Pen Park Road, Bristol. *G. A. Kellaway Coll.*, 1936.
 V. 4015f. A poor specimen. Nr. Redland, Bristol. *W. H. Wickes Coll.*, 1900.

Collection of the Geological Survey and Museum:

- PM. 882. Two poor specimens. (Also catalogued under *Naiadita* and *Hepaticites*.) Bedminster, Bristol.
 56513. A broken specimen consisting of one semicell. (Also catalogued under *Naiadita* and *Botryococcus*.) Crox Bottom, Novers, Bristol. Presented by *G. A. Kellaway*, 1937.

BRYOPHYTA

HEPATICAЕ

Genus **NAIADITA** Buckman emend.

1850 *Naiadita* Buckman, p. 415.

The first published reference to *Naiadita* was contributed by its discoverer, P. B. Brodie, to the second edition of Murchison's "Geology of Cheltenham" (1844, p. 52), where he refers to "a new plant belonging to the family Naiades, or some of its allies; which from its peculiar characters, and the numerous *Cypris* accompanying it, seems to be much more closely allied to a fresh-water than to a marine genus." On p. 81 of the same work Buckman listed the plant as "*Naiadites acuminata* (Brodie)"; this is a *nomen nudum* and had not been published by Brodie. On p. 93 Buckman gave a brief description, without figures, of "*Naiadea acuminata*," together with a diagnosis of *Naiadea*, which, however, had already been used (p. 67) for leaves of the *Podozamites* type from the Stonesfield Slate. His *Naiadea obtusa* (pp. 67, 93; pl. I, f. 2) may be *Podozamites stonesfieldensis* Seward, and *N. ovata* (pp. 67, 94; pl. II, f. 1) may possibly be *Sphenozamites belli* Seward. The genus *Naiadea*, therefore, must be regarded in its first use as a synonym of *Podozamites*, and cannot in any case be applied to our Rhaetic plant. The name *Naiadita* was suggested

by Brodie, who gave it—again without figure or description—in his “Fossil Insects” (1845, p. 93). The first valid use of the name, therefore, is due to Buckman (1850, p. 415). The suggestion of affinity with *Naias* is, of course, unfortunate, and there is also a likelihood of confusion with the well-known genus of non-marine fossil lamellibranchs, *Naiadites*; this variant of the name has in fact frequently been used for the present plant.

EMENDED DIAGNOSIS OF *Naiadita*—Stem slender. Rhizoids unicellular with evenly thickened walls. Leaves borne in a spiral, attached transversely by a broad base, composed of a single layer of cells and without any midrib. Archegonia lateral on short stalks which afterwards elongate and form fruit pedicels; archegonia at first naked, but afterwards enveloped in a perianth resembling a group of foliage leaves. Sporophyte consisting of a spherical capsule (and probably a minute foot); capsule developing to maturity within the archegonium venter and becoming partly embedded in the tissue of the gametophyte pedicel. Wall of capsule composed of one layer of evenly thickened cells; ripe capsule full of spore-tetrads and containing no sterile cells of any sort.

***Naiadita lanceolata* Buckman, emend. Harris.**

(Pls. I–IV; V, figs. 1–3; Text figs. 4–22)

- 1844 *Naiadites acuminata* Buckman in Murchison, p. 81. (*Nomen nudum*.)
- 1844 *Naiadea acuminata* Buckman in Murchison, p. 93. (Inadequate description without figure.)
- 1845 *Naiadita lanceolata* Brodie, pp. 92, 93. (*Nomen nudum*; locality.)
- 1850 *Naiadita lanceolata* Buckman, p. 415, fig. 2.
- 1850 *Naiadita obtusa* Buckman, p. 415, fig. 3.
- 1850 *Naiadita petiolata* Buckman, p. 415, fig. 4.
- 1861 *Naiadita acuminata* Buckman: Moore, p. 514. (Locality.)
- 1862 *Naiades* Jones, pp. 68, 69. (Statement of occurrence with associated Crustacea.)
- 1871 *Naiadites*: Phillips, pp. 102, 105; pl. vii, figs. 22–24. (Redrawn from Buckman 1850.)
- 1876 *Naiadita acuminata* (?) Buckman: Woodward, p. 90. (Mention of occurrence.)
- 1886 *Najadita*: Starkie Gardner, p. 203. (*Naiadita* discussed and regarded as moss.)
- 1886a *Najadita*: Starkie Gardner p. 495. (*Naiadita* stated to be a moss.)
- 1888 *Naiadita lanceolata* Buckman: Prestwich, p. 168, pl. lxxviA. (Drawing from Buckman's figure.)
- 1891 *Naiadita*: Wilson, p. 548. (Stratigraphy of beds with *Naiadita* and some discussion.)
- 1894 *Naiadita*: Wilson, p. 229. (As 1891, republished.)
- 1894 *Naiades*: Jones, p. 156.
- 1894 *Naiadites*: Jones, p. 163. (Statement of occurrence with associated Crustacea.)
- 1898 *Najadita*: Seward, p. 240. (Brief discussion of systematic position.)
- 1900 *Naiadites acuminatus* Buckman: Wickes, p. 422. (Stratigraphy of beds with *Naiadita*.)
- 1901 *Naiadites acuminatus* Buckman: Wickes, p. 100. (Stratigraphy of beds with *Naiadita*.)

- 1901 *Naiadita lanceolata* Buckman: Sollas, p. 307, pl. xiii; text-figs. 1-3. (Description and discussion.)
- 1901a *Naiadita*: Sollas, p. 140. (Summary of above description.)
- 1903 *Naiadita lanceolata* Buckman: Richardson, p. 127 *et seq.* (Stratigraphy of beds with *Naiadita*.)
- 1903a *Naiadita lanceolata* Buckman: Richardson, p. 82. (Stratigraphy of beds with *Naiadita*.)
- 1904 *Naiadita*: Short, p. 171 *et seq.* (Stratigraphy of beds with *Naiadita*.)
- 1904 *Naiadita*: Reynolds and Vaughan, p. 195. (Stratigraphy of beds with *Naiadita*.)
- 1904 *Lycopodites lanceolatus* (Buckman) Seward, p. 14, pl. ii, figs. 2, 3. (Description and discussion.)
- 1904a *Lycopodites lanceolatus* (Buckman): Richardson, p. 532. (Stratigraphy of beds with *Naiadita*.)
- 1904b *Lycopodites* (*Naiadita*) *lanceolatus* (Buckman): Richardson, p. 92. (Stratigraphy of beds with *Naiadita*.)
- 1904c *Lycopodites lanceolatus* (Buckman): Richardson, p. 38. (Stratigraphy of beds with *Naiadita*.)
- 1905 *Lycopodites lanceolatus* (Buckman): Richardson, p. 376. (Stated not to occur in Monmouth.)
- 1905a *Lycopodites lanceolatus* (Buckman): Richardson, p. 417. (Stratigraphy of bed with *Naiadita*.)
- 1906 *Lycopodites*: Richardson, p. 208. (Stated not to occur at Berrow Hill, Tewkesbury.)
- 1910 *Lycopodites lanceolatus* (Buckman): Seward, p. 81, text-fig. 136. (Discussion.)
- 1911 *Lycopodites lanceolatus* (Buckman): Richardson, p. 64 *et seq.* (Stratigraphy of beds with *Naiadita*.)
- 1912 *Lycopodites lanceolatus* (Buckman): Richardson, p. 28. (Mention of occurrence.)
- 1927 *Lycopodites lanceolatus* (Buckman): Hirmer, p. 320. (Summary of Sollas's description.)
- 1929 *Lycopodites*: Richardson, p. 345. (Mention of occurrence.)
- 1933 *Naiadites lanceolata* Buckman: Arkell, pp. 107, 109. (Mention of occurrence.)
- 1934 *Naiadita lanceolata* Buckman: Kellaway & Oakley, p. 473. (Stratigraphy of beds with *Naiadita*.)
- 1935 *Naiadites lanceolata* Buckman: Kellaway, p. 565. (Stratigraphy of beds with *Naiadita*.)
- 1937 *Naiadites lanceolata* Buckman: Kellaway, p. 226. (Stratigraphy of bed with *Naiadita*.)
- 1937a *Naiadita lanceolata* Buckman: Harris, p. 429.

EMENDED DIAGNOSIS OF *Naiadita lanceolata*.—Stem usually not more than 2 cm. high, branched slightly or not at all. Leaves typically lanceolate, 1-5 mm. long; narrower near the base of the plant, rounder near its apex; in mature plant leaves typically borne in a $\frac{3}{8}$ spiral. Cells of leaf typically rectangular, $90\ \mu \times 50\ \mu$, walls delicate, corners unthickened. Rhizoids $55\ \mu$ wide. Archegonium about $300\ \mu$ long, capsule typically 0.8 mm. in diameter; wall cells $45\ \mu$ wide. Spores lenticular, about $100\ \mu$ wide, perispore loosely fitting, forming a marginal wing; its outer side bearing small tubercles, its inner side numerous small spines; exospore thickly cutinised, of nearly uniform thickness apart from a thickened rim.

Gemma cups more or less conical with an entire or deeply

lobed margin, consisting of a unistratose membrane (i.e., composed of a single layer of cells) resembling the leaves. Gemma oval, typically $400\ \mu \times 220\ \mu$, two cells thick in the middle, one cell thick towards the margins, cells about $40\ \mu$ in diameter. Germination apical.

N. lanceolata is thought to have been a submerged fresh-water plant.

HORIZON.—*Naiadita* Bed; Upper Rhaetic.

LOCALITIES.—English Rhaetic outcrop from Somerset east of Mendip Hills to Worcestershire and Warwickshire—see pp. 4-5.

TYPE.—The specimen figured by Buckman (1850, p. 414, fig. 2) as *Naiadita lanceolata* "Brodie" may be taken as the type. According to an old label, V. 3357 is said to be the original of both figs. 2 and 3, but neither of them can now be clearly recognised. It is probable that these figures are to some extent restorations, especially as fig. 4 is certainly a composite drawing based on two counterparts numbered V. 3356.

DESCRIPTION.—*The general nature of the material.* *Naiadita* is represented by a wonderful abundance of specimens. Rock providing unbroken plants is, it is true, known from only a few places near Bristol where there is now no exposure (Pl. I, fig. 3), but rock with broken but well-preserved specimens, such as I have collected, appears to be widespread (Pl. I, fig. 2). The abundance of specimens on the split surface of the rock may be realised from these figures of a count of recognisable organs or their fragments on a typical square centimetre:

Rhizoid fragments . . .	40
Leaves and leaf fragments . .	33
Gemmae . . .	3
Detached archegonium . . .	1
Sporangium wall cells . . .	1

So far as I know this is typical over a large part of a stretch of about 90 miles.

Another reason favouring the study of *Naiadita* is that its associates are few, rare by comparison, and very different in appearance. Thus risk of confusion should be small. The main difficulty is that in certain layers *Naiadita* specimens are so abundant as to overlap and it may be difficult to see that they are not actually joined. Thus while the attachments of leaves, rhizoids, gemma cups, and archegonia to stems, which are illustrated by very many specimens, are hardly open to doubt, there is a real possibility that I may be mistaken in describing certain other attachments, in particular the gemma to the cup. The specimen illustrated in Pl. II, fig. 3, for example, is the clearest of a very few which seem to show this attachment, but it may be that the presence of the gemma in the cup is accidental.

Stem. The stem is often nearly straight, and shows no sign of a creeping base. The longest stem found is 3.2 cm., but very few are over 2 cm. long, many apparently mature and complete specimens being much shorter. The thickest stems are $500\ \mu$ thick, the majority of large plants have stems $200\ \mu$ thick (about four cells thick), the smallest are $50\text{--}100\ \mu$ thick. In complete specimens the stem becomes somewhat narrowed towards the base.

Most stems are unbranched (apart from the production of gemma cups), but a few are forked (one specimen forked twice) in the middle or upper part of the plant, and there is good reason to suppose that nearly every stem represents a separate plant.

The cell structure is seen in all specimens, though often obscurely. In rather slender, semi-petrified stems (Text-fig. 7 *E*) all the cells can be seen distinctly by careful focusing: they are parenchymatous, $100\ \mu$ long (occasionally $200\ \mu$ long) and $50\ \mu$ broad. The inner cells appear to be just like those of the outer layer. In stems preserved as pure compressions the appearance suggests a thick-walled prosenchymatous core surrounded by a delicate epidermis. I consider this appearance to be the natural result of the compression of a parenchymatous cylinder; the margins, where one to two layers alone are crushed, will show their cells distinctly, while in the inner part, where several layers and many walls are involved, the whole compressed mass will appear much subdivided, and the somewhat elongated shape of the cells will make most of these subdivisions longitudinal. This is referred to later when Sollas's interpretation of the stem is discussed. The cells of the stem are placed end to end in well marked longitudinal rows; these rows seldom show any trace of twisting. Nevertheless, a few twisted stems were seen, and the constant diameter of such stems indicates that they were originally round, not flattened.

The leaves are purely transverse—never oblique or longitudinal—in their attachment to the stem (Text-fig. 7 *D, E*). The leaf is continuous with the surface layer which its cells closely resemble in character. It is often possible to make out almost exactly where (i.e. on which side) the leaves are attached to the stem and it can then be deduced that their attachments are always spiral. In favourable specimens (Text-figs. 4–6) an arrangement in close agreement with a $\frac{3}{8}$ spiral can be discerned—if an ideal stem with leaves in such a spiral is reconstructed and then imagined to be flattened the result corresponds with the fossil. The attachments may indeed conform even more closely to some other fraction, but none of the lower fractions of the ordinary phyllotaxis series, $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, . . . , fits as well as $\frac{3}{8}$.

Rhizoids. Every complete plant bears a considerable number—thirty or so—of rhizoids, and large numbers of detached rhizoids

and fragments occur everywhere. The great majority are of nearly constant diameter, 50–60 μ ; in young plants they are more



TEXT-FIG. 4. *Naiadita*.

Outline drawing (to the left) and restoration (to the right) of a leafy shoot. In the restoration the leaves are numbered on the basis of a $\frac{3}{8}$ counter-clockwise spiral. Specimen V. 4015a, $\times 9$.

slender, and a few isolated thicker ones were seen which may belong to this species. The rhizoids are never branched, are

uniform in diameter, and never show septa, nor local thickenings such as tubercles. They are almost straight, apart from occasional sharp bends and folds which appear to have been caused



TEXT-FIG. 5. *Naiadita*.

Outline drawing (to the left) and restoration (to the right) of a leafy shoot bearing a gemma cup and an archegonium with a perianth. In the restoration the leaves are numbered on the basis of a $\frac{3}{8}$ clockwise spiral. Reading Univ. Geol. Coll., No. 3845, $\times 9$.

in preservation. They never appear to be moulded around grit particles.

Towards the free end the walls of the rhizoid become more and more delicate and finally cannot be distinguished; the end itself has not been recognised, and the length cannot therefore

be stated with certainty, though presumably it is only a little more than what is seen. This means that the rhizoids springing from the base of the stem would be about 5 mm. long; those springing higher up are longer, since they seem to reach down to about the same level.



TEXT-FIG. 6. *Naiadita*.

Outline drawing (to the left) of two partly overlapping shoots and restoration (to the right) of one of them. The leaves up to the ninth are numbered on the basis of a $\frac{3}{8}$ clockwise spiral. The existence of the leaf indicated by a dotted line is doubtful. V. 4015c, $\times 7$.

Rhizoids seem to spring in greatest abundance from the slender base of the stem, but many also arise a centimetre or even more above the base and pass down the stem as a loose mantle among the leaf bases. In mature plants it is usually very difficult to see exactly where rhizoids are attached because they conceal one another. They are, however, well shown in worn stem fragments

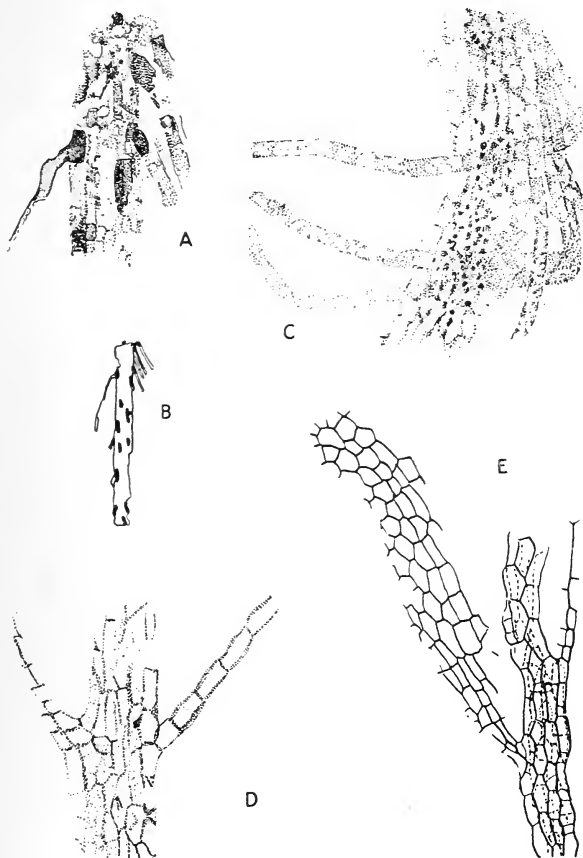
where most of the leaves and rhizoids are broken off near their bases. In such specimens all the surface cells may be equally thick, but in others the cells giving rise to rhizoids (Text-fig. 7 A, B) are much darker than the rest. In young plants, too, where most of the stem cells are very delicate those forming rhizoids are somewhat thickened and hence conspicuous (Text-fig. 12 C). Rhizoids never arise from the leaves, nor, unless I have misinterpreted the "gemma-stalk," do they arise directly from the gemma.

The Leaf. The dimensions of the leaves and their relative width vary within wide limits. In well-developed stems the lowest leaves are almost linear, the next are rather longer and much broader, being as a rule lanceolate, and towards the apex they are shorter and often wider still (Text-figs. 5, 6), in some specimens being almost round. Some stems also bear leaves which are altogether larger than those of others: the longest leaf seen was 7 mm. long, but the great majority are under 5 mm. long. The leaf lamina is somewhat incurved and in a few (presumably immature) plants the upper leaves are bent over the apex as in a bud.

The leaf (Text-fig. 8) is always one cell thick; its base is rather narrowed, and no midrib is present. The basal cells are small, but not otherwise specialised; the other cells are uniform, except that the marginal cells are often half the normal size. The marginal cells have a delicate outer wall, and often bulge somewhat, but never enough to form teeth. The cell which occupies the leaf apex (apical cell) is only distinguished from the other marginal ones by its position; it is referred to later. In certain leaves, occasional cells are full of minute concretions of ferric oxide, but there is no reason to suppose that these cells were originally different.

The leaf cells have rather delicate walls which are usually of quite even thickness; in certain leaves, however, patches of brown material sometimes occur on the lateral or surface walls which may represent local thickenings in the original wall. The arrangement of the leaf cells is often characteristic: over most of the leaf they form transverse and longitudinal rows, which appear to be related to the manner of cell division. By comparing the arrangement of the cells in a series of narrow or broad leaves, a picture can be drawn of the manner in which the cells divided (Text-fig. 9). In the narrowest leaves the apical cell comes first, then a uniseriate stretch, then division of these cells to give a biseriate filament. In slightly broader leaves the uniseriate stretch is shorter and the biseriate stretch is followed by further subdivision of the cells. In still broader leaves the same stages seem to have been passed through, but the cells of the uniseriate filament subdivide at once and only the apical cell retains its

identity, though the transverse cell-rows mark the original division walls. Finally, in some round-topped leaves even the apical

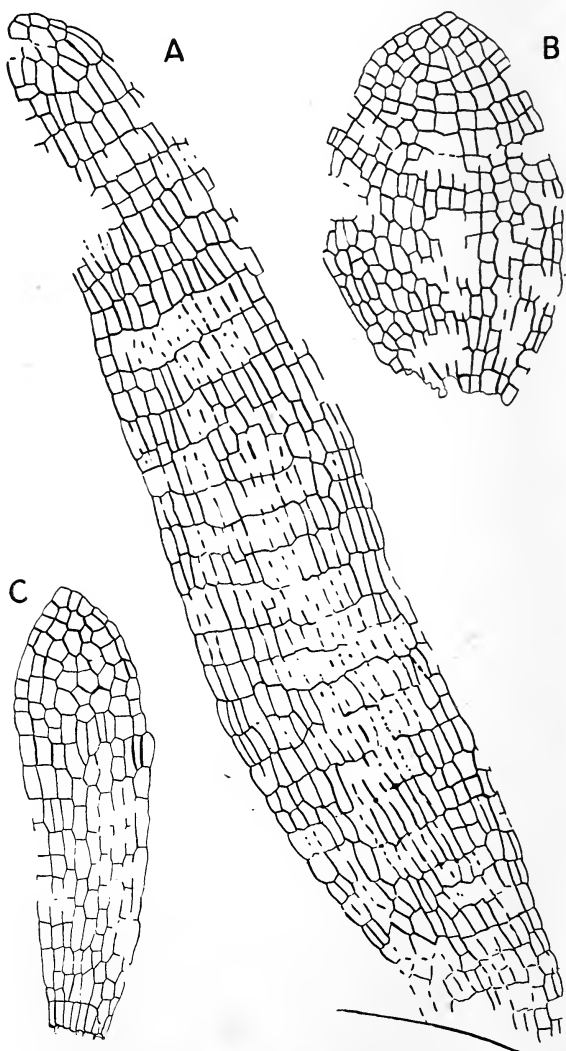


TEXT-FIG. 7. *Naiadita*.

A, upper part of a worn stem showing the origin of rhizoids from thickened cells, V.25281, $\times 45$. *B*, the whole stem fragment represented in *A*, $\times 15$. *C*, lower part of a leafy stem bearing rhizoids. The stem appears to possess an epidermis and a core of different structure (see p. 50); V. 4015a, $\times 45$. *D*, part of a slender leafy stem showing the attachment of two leaves; Reading Univ. Geol. Coll., 3845, $\times 45$. *E*, slender calcified stem bearing two leaves. The various layers of cells of the stem are indicated; the cells with firm outlines are situated on the upper surface; V. 24810, $\times 45$.

cell has undergone longitudinal subdivision and is unrecognisable, though transverse rows are to be seen as before (Text-fig. 9 *B*, *C*). It will be noticed that on this interpretation the transverse rows are regarded as fundamental, while the longitudinal ones result

merely from an equal number of divisions occurring in successive transverse segments.

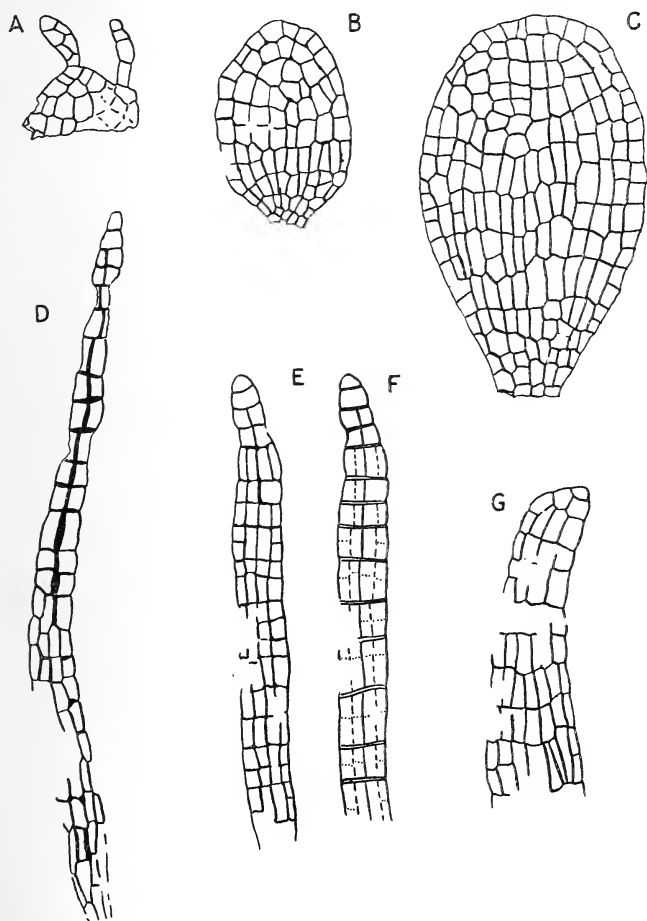


TEXT-FIG. 8. *Naiadita*—typical leaves.

A, greater part of a large leaf (the base is concealed by the stem), V. 4015 c, $\times 45$. B, smaller and broader leaf, V. 24809, $\times 45$. C, small and narrow leaf, V. 24810, $\times 45$.

Towards the apex of the leaf, especially in the broader leaves, the "transverse" cell-rows cease to be straight and become more

and more arched. These arched rows suggest that the apical cell has been dividing by a curved wall parallel to its base. In some of the broadest leaves all the cell-rows are arched and then the

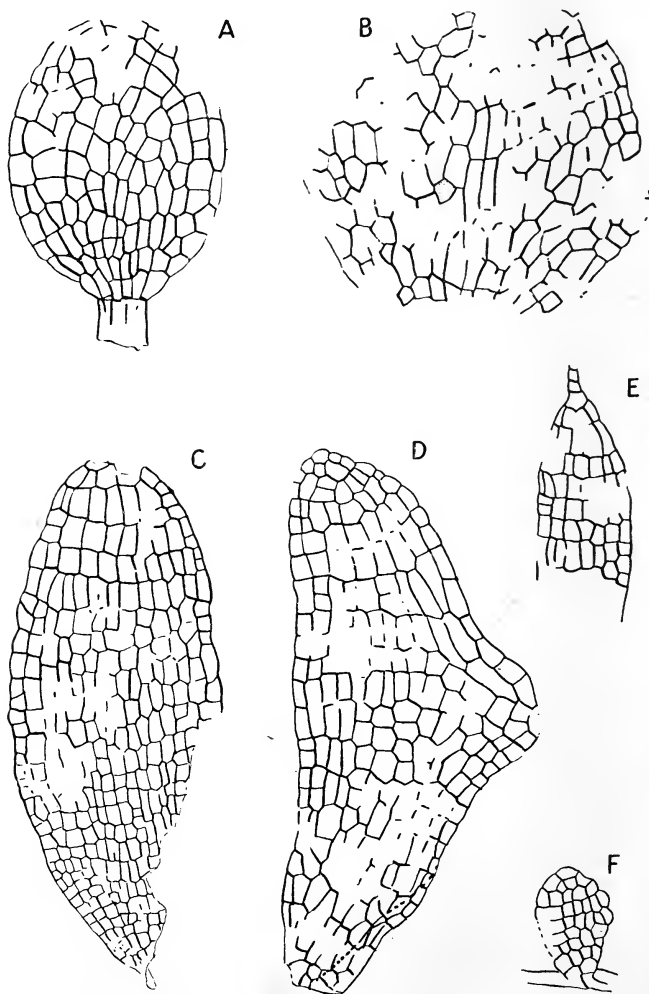


TEXT-FIG. 9. *Naiadita*—leaf.

A, large fragment which appears to be proliferating, V. 24810, $\times 50$. B, small leaf with no distinct apical cell, V. 11010 d, $\times 50$. C, as B, V. 11010 c, $\times 50$. D, very narrow leaf, V. 4015 c, $\times 50$. E, narrow leaf, V. 25272, $\times 50$. F, diagram of the leaf represented in E showing the possible order of cell-wall formation. G, upper part of a leaf 3 mm. long, V. 25271, $\times 50$.

cells along the middle line of the leaf (which naturally point longitudinally) have some resemblance to a midrib (Text-fig. 10 B). In a good many leaves the cells over a considerable part cannot

be analysed into transverse rows, but it is significant that no other regular arrangement apart from the one described is ever found (see p. 53).



TEXT-FIG. 10. *Naiadita*—abnormal leaves.

All $\times 45$.

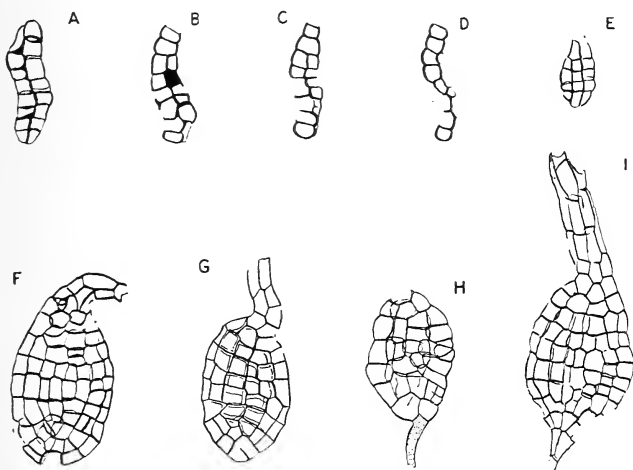
A, rounded leaf showing the very oblique cell-rows, V. 4015 b. *B*, very broad leaf with longer cells in the middle suggesting a midrib, V. 25278. *C*, leaf which appears to show a basal meristem, V. 25282. *D*, lobed leaf (the base is folded on itself), V. 25277. *E*, upper part of leaf which appears to be proliferating (the leaf is 2 mm. long), V. 25275. *F*, very small leaf with unusually small cells, V. 24810.

Leaf Abnormalities. Great numbers of leaves were examined, and it is not surprising that a few abnormal specimens should have been found. These abnormalities fall into the following groups.

(1) Imperfect shape. Occasionally one side of a leaf has developed more than the other, giving a sickle-shaped leaf, or has formed a broad lateral lobe in which an "apical cell" can be distinguished (Text-fig. 10 *D*). No leaf shows, however, a well-balanced dichotomy.

(2) The cells in the lower part of the leaf are small and have thin walls, appearing, in fact, meristematic (Text-fig. 10 *C*). I think it likely that these leaves grew by an intercalary meristem, and it is possible that this is normal in the larger leaves, though seldom preserved.

(3) A leaf fragment was found in which the apical cell and another marginal cell have proliferated. Presumably these would have formed new plants (Text-fig. 9 *A*). The specimen shown in Text-fig. 10 *E* is possibly similar.



TEXT-FIG. 11. *Naiadita*—gemmae.

All $\times 45$.

A, B, C, D; a gemma preserved in side view. Successive levels have been exposed by rubbing away rock chiefly from the middle portion (specimen finally destroyed). *E*, a small gemma, V. 25284. *F*, a large gemma with a basal notch, V. 25276. *G*, a gemma with an entire base, V. 11010 c. *H*, gemma with a unicellular stalk, V. 24810. *I*, large gemma with a tapering end, V. 25274.

Gemmae. Great numbers of gemmae were seen: in certain bedding planes they are some of the commonest fossils. They

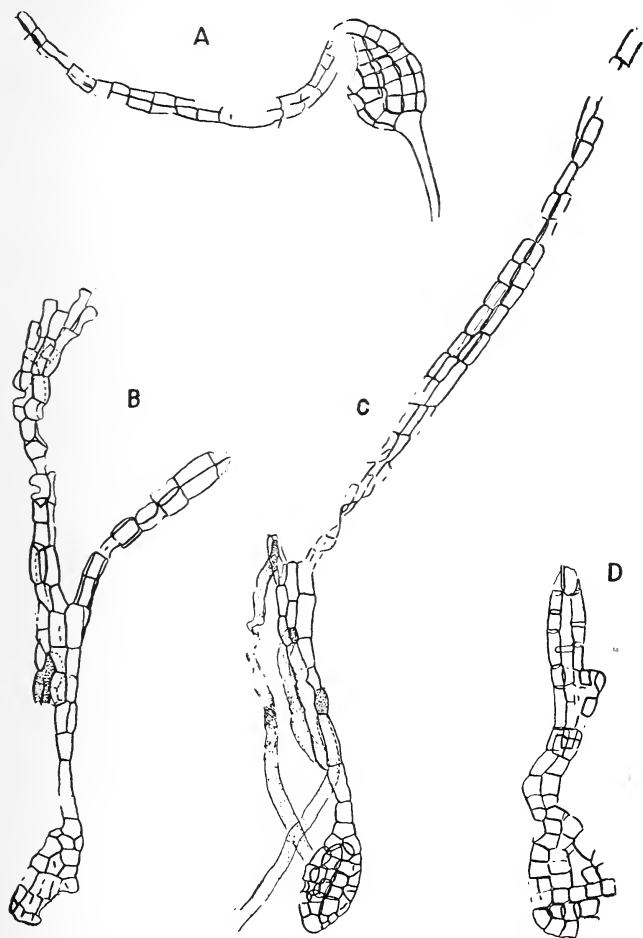
are oval, varying in dimensions from $500\ \mu \times 300\ \mu$ to $200\ \mu \times 120\ \mu$. Apart from differences due to this variation in size, their structure is nearly constant (Text-figs. 11, 12). They are composed of squarish cells about $45\ \mu$ wide, arranged in more or less regular transverse and longitudinal rows. The margins are always one cell thick; the inner part is always considerably thicker than the margins and, as far as I know, is always two cells thick; the cells of the upper layer are generally opposite those of the lower, and thus often difficult to distinguish unless the gemma happens to lie slightly obliquely. A peculiar character of the gemmae is that their cells are partially or even completely filled with calcite (i.e. the gemma is "petrified"): this petrification has occurred even where the stem and leaves are preserved with scarcely any filling.

The great majority of gemmae are isolated. The only ones definitely associated with the parent plant are found in the terminal cups, which I have therefore termed gemma cups, and in the absence of evidence to the contrary I assume that they were all borne in these cups. Certain gemmae have a slender unicellular outgrowth or stalk from the basal end (Text-fig. 11 H), but the great majority show no such feature; the marginal cells either being complete at the base, or one cell being absent and so forming a basal notch. Of the gemmae situated inside cups (and believed to be attached) one shows the gemma at the base of the cup (Pl. II, fig. 3) and others at a short distance above the base, though here no stalk could be discerned. I am thus doubtful whether this outgrowth should be regarded as a stalk or a rhizoid, but in any case the great majority of gemmae were certainly shed without any stalk and no remains of stalks can be seen in the cups.

The apical cell of the gemmae can seldom be seen because nearly all the best preserved detached gemmae have obviously germinated, and those still in the cups while ungerminated are not very favourably placed for detailed study. I am doubtful whether I have recognised the apical cell at all.

Germination of the gemmae is normally apical, and is always "direct," that is, it gives rise to a leafy plant, though this is altogether more slender than the mature plant. The stem of the young plant may be one, two, or three cells thick at its base, being thicker where the gemma is large. There is much variation in the form of these young plants, the first internode being sometimes long, sometimes short, and not infrequently sharply bent as though the young plant had grown up from an inverted gemma. Several gemmae were found which had given rise to two embryos. No rhizoids were seen rising directly from a gemma (unless the stalk-like organ shown in Text-fig. 11 H is a rhizoid), but rhizoids may spring from very near the base of the young plant.

Many gemmae look rather like antheridia (Text-figs. 11 F, G). Undoubtedly those which bear an embryo, and those which are



TEXT-FIG. 12. *Naiadita*—germinating gemmae.

All $\times 45$.

A, stalked gemma bearing an embryo with a single leaf, V. 25273. B, the embryo has a single imperfect leaf (with a twisted base) to the right, and there is probably the base of a leaf lying over the stem apex to the left, V. 24810. C, the embryo stem is uniseriate at its base and bears three rhizoids and a well developed first leaf, V. 24810. D, embryo showing what appears to be a stem apex, V. 25279.

unmistakably two cells thick in the middle and one cell thick towards the margin, are true gemmae, but such unmistakable

specimens are in the minority, both of those still occurring in the cups and those isolated.

Embryo. The abundance of young plants is remarkable: they are, in fact, commoner than mature ones. So far as I know this is without parallel for fossil plants, in which seedlings and sporelings are very seldom found (in spite of the fact that plant mortality is highest among seedlings).

Just as the presence in a deposit of young as well as mature stages of marine shells suggests that the fossils accumulated in their original habitat, so the abundance here of young plants indicates that *Naiadita* was a water-plant which flourished where it is now preserved.

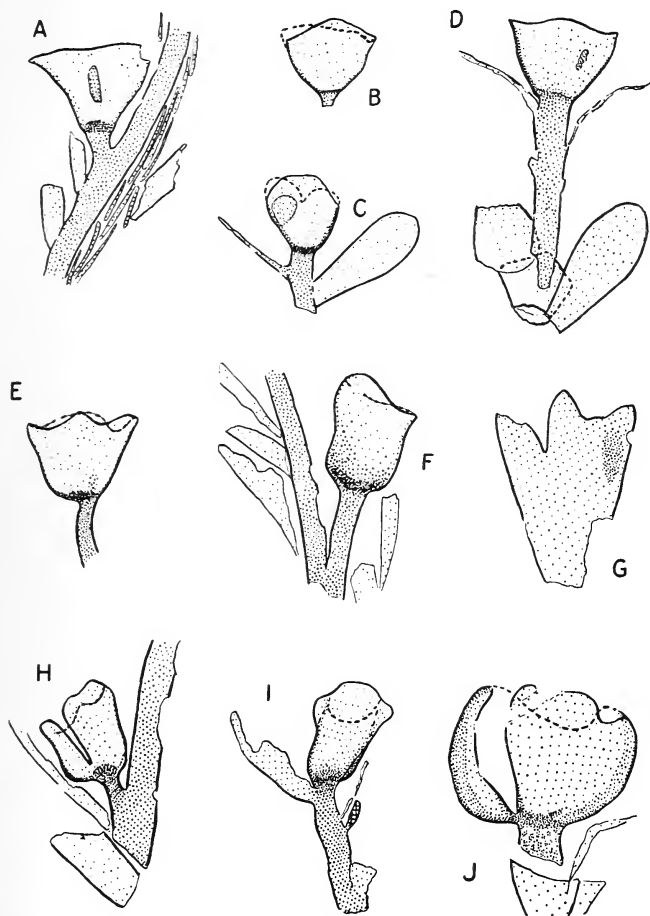
Many of these embryo plants are only fragments, but in the numerous cases where their origin could be clearly seen all arose from a gemma. Despite careful search, I found no example of a germinating spore or tetrad, or of a young plant with a spore coat attached to it. So many spores are scattered through the rock that this almost seems surprising. The embryos being of more delicate texture than the mature plants are more difficult to investigate, but the great number available compensates for this. As has been stated, the embryo is always formed from the apex of the gemma (where this is distinguishable), but it often bends sharply at its base. The base of the stem may be from the first a column of two or three cells thick, or it may be at first uniseriate, but becoming thicker above. Rhizoids spring from the axis even below the first leaf; they are rather more slender than the rhizoids of the mature plant, and the cell from which they spring is considerably darker than the neighbouring cells.

Embryos are very often preserved at the stage when they have their first leaf. This leaf arises 0.5 mm. or more from the gemma, and at this stage appears to continue the axis, the stem apex appearing as a lateral cluster of cells. The first leaf is of very considerable size in relation to the young plant, being two or three cells wide in the lower part, but it becomes narrower and finally filamentous towards the apex. It is about a millimetre long.

In older embryos later leaves are more or less developed, reaching a larger size than the first leaf. In most of the embryos the internodes are some of the longest ever produced by the plant, and of course much the most slender.

The preservation is scarcely good enough to allow a definite statement to be made about the structure of the stem apex beyond showing its appearance in drawings, and for the same reason it would be a mistake to assume from its appearance that the apex is really lateral and the first leaf terminal—it may perhaps be pushed aside by the precocious development of the leaf. On the other hand, in the development of the gemmae there

is no real protonemal nor thalloid phase, and this has some taxonomic importance.



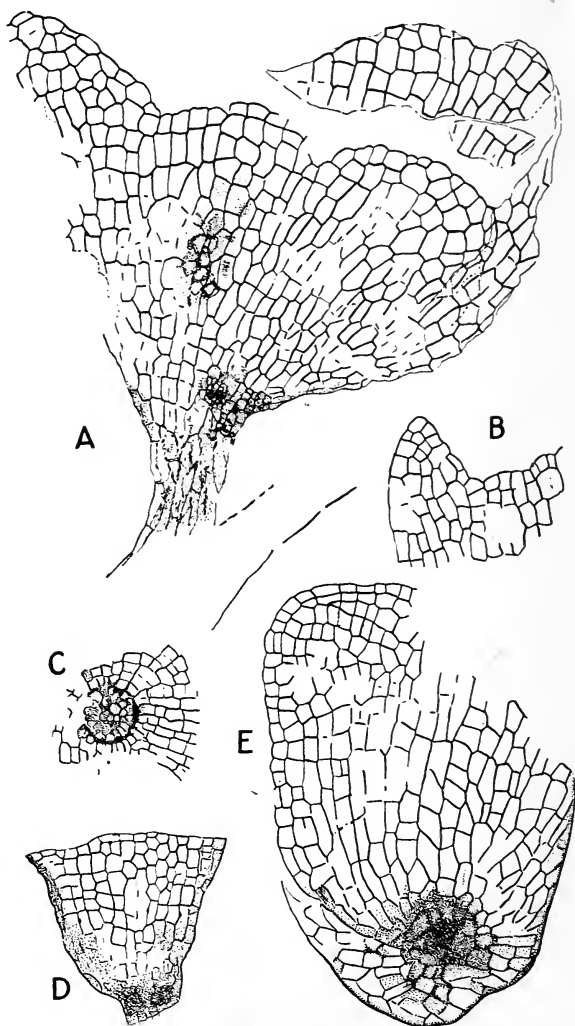
TEXT-FIG. 13. *Naiadita*—gemma cups.

All $\times 45$.

The figures are outline drawings, the stippling being semi-diagrammatic. A broken line at the mouth of the cup represents the upper margin which was dissected away to expose the lower margin (shown by a firm line). Gemma-like bodies are seen in *A*, *C*, *D*; in *A*, the stem is accompanied by rhizoids, and in *I* it bears a small lateral organ of doubtful nature.

A, Geol. Surv. & Mus., No. PM. 877 C (6094). *B*, V. 25281. *C*, Bristol Museum, No. Ca. 7687. *D*, V. 25280 (part of a second cup is seen below). *E*, Geol. Surv. & Mus., No. PM. 877 A (6094). *F*, Geol. Surv. & Mus., No. 877 C (6094). *G*, V. 24812. *H*, Geol. Surv. & Mus., No. 877 A (6094). *I*, Bristol Museum, Ca. 9279. *J*, V. 24812.

Gemma Cups. Most of the more complete stems bear a cup-shaped organ which I interpret as a gemma cup; some bear more



TEXT-FIG. 14. *Naiadita*—structure of gemma cups.

All $\times 40$.

A, a rather large cup. The tissue above probably represents part of this cup; the dark body to the left of the middle is possibly a gemma, V. 4015 c. *B*, part of the toothed cup shown in Text-fig. 11 *G*, V. 24812. *C*, basal part of a cup, V. 25285. *D*, rather small cup, V. 25270. *E*, oblique view of a cup which is split down one side, V. 25283.

than one. Such cups have a stout stalk which may either be the obvious termination of the stem or may appear to be a lateral branch. In all cases it is possible to regard the cup as terminal, but pushed more or less aside by a strong branch which may represent a dichotomy or possibly a true lateral branch.

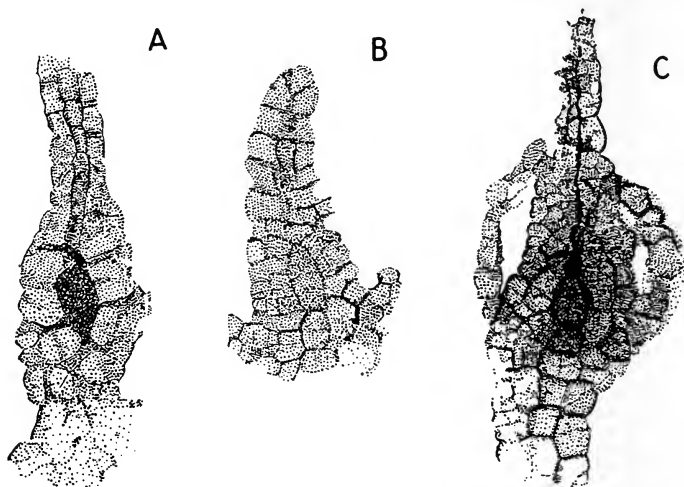
The cups themselves vary much in size and shape, as will be seen from Text-fig. 13. Perhaps the commonest type is one approximating to Text-fig. 13 *E*, but many others also are common. The stalk has exactly the character of an ordinary stem and may bear leaves just below the cup. The cup itself is formed of a membrane, one cell thick, of cells 50–100 μ long and 30–60 μ wide, which in all their characters resemble the cells of the leaves. Their arrangement is not, however, quite the same, as the tendency to form longitudinal rows is more pronounced, and only near the free margin do they form distinct transverse rows. The arrangement suggests that the cup grew by a marginal or intercalary meristem.

The margin of the cup is interesting. It is seldom entire, but is more or less deeply lobed into two to four segments, and not infrequently may be split to the base at one point. One specimen (Text-figs. 13 *G*, 14 *B*) with an unusually pointed lobe shows in this lobe the cell arrangement of a typical leaf, and the lateral margins of the split cup are just like those of leaves (Text-fig. 14 *E*). This agreement suggests the morphological comparison of the gemma cup and leaf, and I suggest that the cup in *Naiadita* may be regarded as the "morphological equivalent" of a number of foliage leaves in the same sense as the gemma cup of the moss *Tetraphis* is regarded as a group of leaves.

The basal cells of the cup are small and cubical and often have dark contents; it is certainly here that the reproductive organs were borne. Unfortunately the majority of cups are quite empty—apart from matrix—and their nature is conjectural. A number, however, contain an oval cell-mass which agrees exactly in the character of its cells with a typical gemma, and such specimens can be confidently regarded as gemma cups (Pl. II, fig. 3). A few show one or more oval bodies (Text-fig. 14 *A*) with altogether indefinite cellular characters; these might well be ill-preserved or immature gemmae, but might also represent delicate-walled antheridia. These specimens are not definite enough to be described or figured in detail.

Archegonia. Mature archegonia are surprisingly common, in fact, about one well-preserved shoot in ten shows them, and detached archegonia are also common. They are often impregnated with calcite. Stems bearing archegonia usually show three or four, borne singly on small stalks which occur on all sides of the stem, at some distance from a leaf. They may possibly replace leaves in the spiral sequence, and are certainly not axillary. The

archegonium is $250\text{--}300\ \mu$ long with a venter $100\ \mu$ wide. The venter wall sometimes consists of a single layer of cells, but sometimes it appears to be composed of two layers—an appearance which may result from the superposition and compression of the different wall cells, but might also be due to its becoming two-layered with age. The cavity of the venter is usually full of black material. The neck is a tube composed of a single layer of cells; the neck appears to show canal cells, but these doubtless are merely wall cells seen behind the dark contents of the canal.



TEXT-FIG. 15. *Naiadita*—archegonia.

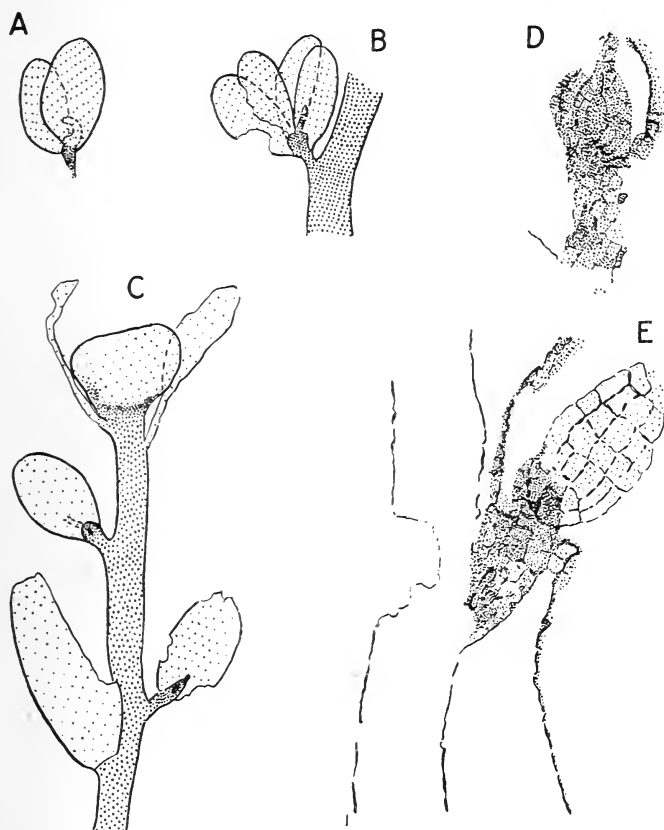
All $\times 160$.

A, no perianth is present, V. 24810. *B*, a small perianth is present, the interior is not as dark as usual, V. 24810. *C*, the perianth surrounds the venter, V. 25286.

I attempted to determine whether the archegonial neck has five or six tiers of cells by carefully rubbing away the material of a petrified archegonium which lay very obliquely in the rock, so as to obtain "serial sections"; but the result was not convincing.

While a good many archegonia are naked, others have a "perianth" of small leaf-like lobes. These perianths show a range in size which I interpret as representing stages in development, though this is not correlated with changes in the archegonium. The first stage consists of some cellular outgrowths just below the venter (Text-fig. 15 *B*) (the archegonium is thus sessile). At the next stage the perianth consists of little scales which grow up round the venter, often very unevenly (Text-fig. 15 *C*), and then at the next stage they have overtopped the neck and form a globular investment round the archegonium (Text-fig. 16). There is now a gap in the series, and the final stage consists of

the perianth of the mature fruit described below. These changes are brought about by enlargement of the cells (from $25\ \mu$, growing to about $100\ \mu$ long), and by a very great increase in their numbers; both changes occur progressively through the series.

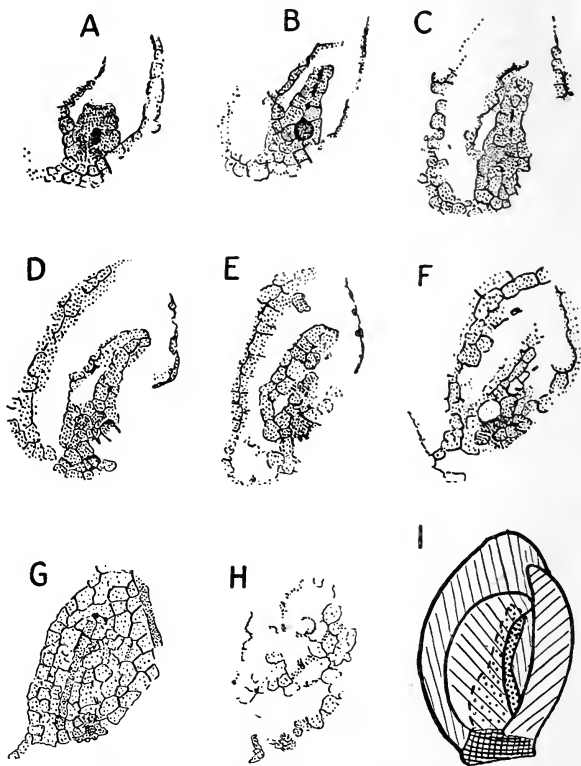


TEXT-FIG. 16. *Naiadita*—perianth.

The drawings A–C are outline drawings with semi-diagrammatic shading. The specimens were dissected and the broken line represents the structure exposed by the removal of upper layers. A, Bristol Museum, No. Ca. 9279, $\times 18$. B, Bristol Museum, Ca. 7687, $\times 18$. C, specimen with two perianths and a gemma cup, Bristol Museum, No. Ca. 9279, $\times 18$. D, archegonium with a perianth only slightly larger than the venter, V. 4015 b, $\times 60$. E, archegonial branch showing three perianth leaves and probably the base of the archegonium; one perianth leaf is bent back; V. 4015 c, $\times 60$.

During the earlier stages it is evident that the different leaves of the perianth arise at different levels (Text-fig. 17); at maturity they seem to form a whorl, but they are probably of different sizes.

The development of the fertilised archegonium is shown very incompletely. Despite careful search only one ill-preserved specimen was found which shows archegonia with partly swollen venters. Almost all the specimens of perianths were "dissected" by scraping away the rock and overlying perianth leaves, but



TEXT-FIG. 17. *Naiadita*—archegonium and perianth.

A-H, successive "sections" obtained by rubbing away the material of an archegonium. The vertical distance between successive levels averages about 10 μ . Note the difference in level of attachment of the perianth leaves on the left. I, restoration based on these sections, $\times 60$. Specimen destroyed, original on V. 4015 a.

their archegonia were no more developed than those figured in Text-fig. 15, except that the neck was sometimes broken down. I regard these archegonia as abortive or unfertilised; in recent Bryophytes such archegonia are often very resistant and may last a long time and, as in the fossil, the venter and neck become full of dark-coloured contents. If this is right, then development of the perianth must proceed to some extent independently of

fertilisation: for this, too, there are numerous analogies among recent Bryophytes.

Later Stages: the Calyptra. Though there is a gap in the sequence between the ripe archegonium and the mature sporophyte, the changes are not too great for the intermediate stages to be imagined. In the specimens with ripe attached sporophytes, the sporophyte is deeply sunken into the tissue of the axis (or this might be better said to have grown up round the sporophyte), and the perianth leaves spring from half-way up the capsule instead of from the base of the archegonium. The cup of tissue round the sporophyte appears to be composed of a few—perhaps two or three—layers of thin-walled cells. The calyptra itself is more delicate and can, indeed, only be recognised with certainty where the archegonium neck is present. It closely envelops the sporogonium wall and its cell structure was not made out.

In the detached sporogonia no trace of the calyptra is present.

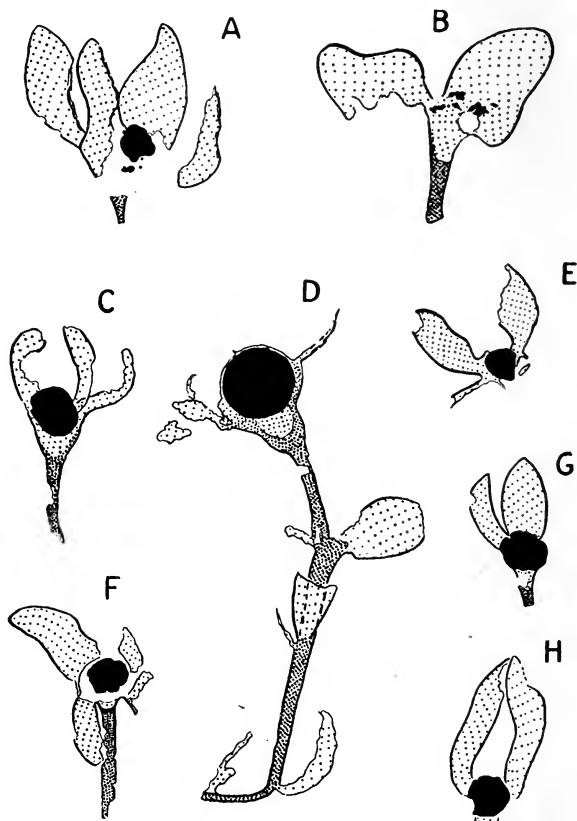
The Pedicel. There seems a distinct correlation between the growth of the perianth and of a pedicel which carries up the whole archegonium and its perianth. In the mature capsule the pedicel is about 2 mm. long and 0.25 mm. thick. It is composed of thin-walled, slightly elongated cells and is just like a slender stem, except that it bears neither leaves nor rhizoids. Near the top it expands greatly where it surrounds the base of the sporophyte, and in one specimen it is perceptibly darker just below the sporophyte foot than elsewhere.

Sporophyte. Mature sporophytes are common in the material from Redland, Bristol (Pl. I, fig. 1), but in other places they are rare except as broken pieces. No immature sporophytes occur, but the mature ones are in various stages of disintegration.

Only one specimen shows the sporophyte attached to a leafy shoot, but Miss Sollas examined two such specimens in one of which it seemed to her axillary, in one terminal. I found, however, a fair number of pedicels bearing perianths and sporophytes (the best of which are drawn in Text-fig. 18), a still larger number of isolated but intact capsules, while spores and fragments of the capsule wall occur in thousands.

The Foot. In specimens where the sporophyte is attached to the gametophyte pedicel the part which I describe as the sporophyte foot is often conspicuous. The pedicel has the structure of an ordinary slender stem, and its tissue is not appreciably calcified, but just below the capsule the pedicel becomes broader and stands out because it contains a considerable mass of calcite. The tissue of the pedicel in front of this mass of calcite shows its cells much more clearly because fewer layers are crushed together

(Text-fig. 19). A number of specimens were sacrificed in an attempt to make out the nature of this calcite mass, but without much result. When the cells above it are etched, or rubbed away with a needle, the calcite appears quite clean and white; it shows no definite trace of cell walls and is also free from the



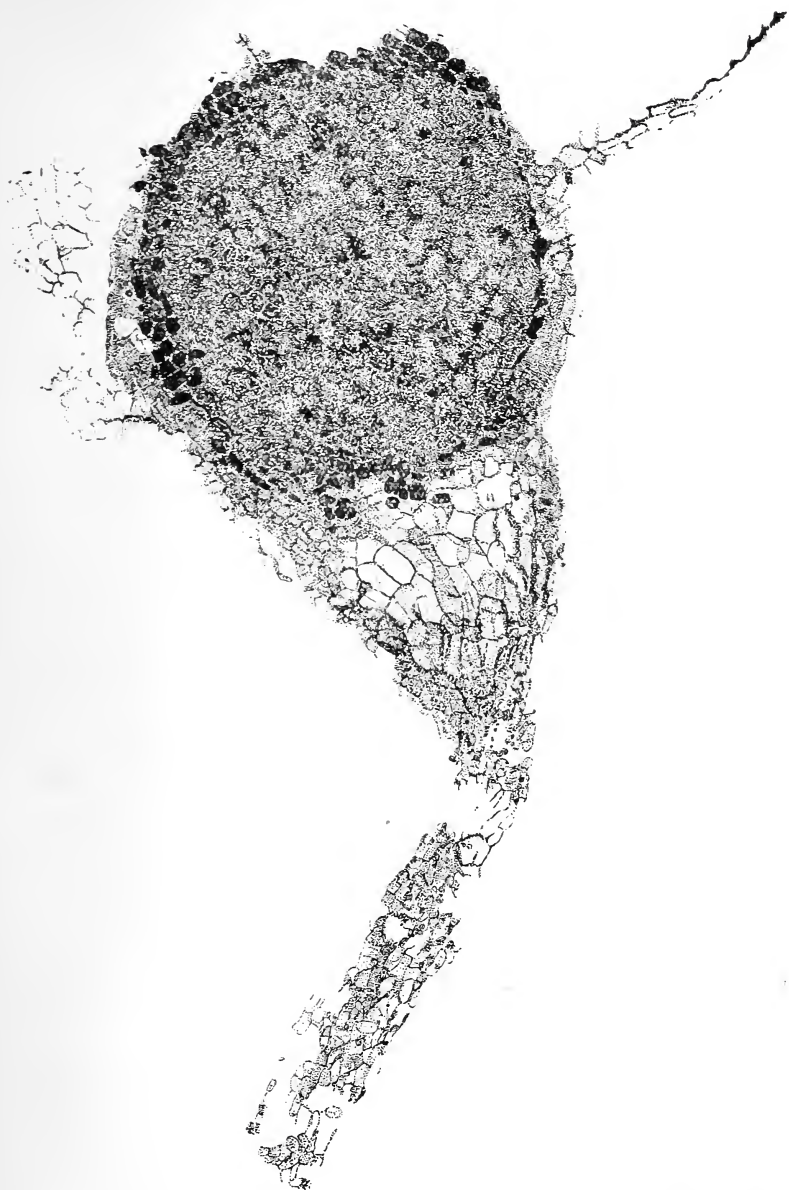
TEXT-FIG. 18. *Naiadita*—ripe fruit and perianth.

The figures are outline drawings with semi-diagrammatic shading, all $\times 7$. A, Bristol Museum, No. Ca. 9278. B, only fragments of the fruit wall are present, V. 11010 b. C, V. 11010 a. D, Bristol Museum, No. Cb. 2663. E, V. 11010 b. F, No. V. 11010 b. G, V. 4015 b. H, V. 11010 b.

particles of silica grit which occur in the ordinary matrix. The whole mass of calcite can be removed without disclosing any structure until the pedicel tissue on the lower side is reached.

Among possible interpretations of this mass of calcite the following may be considered:

(1) There might be an empty space below the capsule which



TEXT-FIG. 19. *Naiadita*—sporophyte.

Drawings showing the appearance of the best specimen (see also Text-fig. 18 *D*). The wall of the sporangium has partly broken away; its cells are shown in solid black. Note the clear tissue in the foot region (the cells shown are those of the pedicel lying in front of the foot). Bristol Museum, No. Cb. 2663, $\times 45$.

became filled with calcite. This I consider improbable because one would expect such a closed cavity to flatten when fossilised, not to become full of infiltrated calcite, and also because this seems a most unlikely place for a cavity to occur.

(2) Presumably, therefore, this region was occupied by cellular tissue which became entirely replaced by calcite, its walls not being preserved. This tissue might be (a) a special region of the pedicel (i.e. gametophytic), in which case the sporophyte would be spherical and without a foot, or (b) the "foot" of the sporophyte, and since the shape of the cavity rather resembles in its form the foot in various living Bryophytes, I have used this latter hypothesis in my description.

The dissection of the base of the capsule has established that there is no "seta" or narrow stalk of hard tissue such as is found in *Riella*. It is most unlikely that such an organ could fail to be preserved, and if preserved fail to be recognised.

The Capsule. About fifty more or less complete capsules were examined. They range in size from 0.3 mm. to 1.2 mm. wide, about 0.8 mm. being the normal size. A considerable number of these capsules were macerated and no differences in detail were found between the large and the small ones, their wall cells and their spores being of the same size and structure.

All the capsules are impregnated with calcite, and in most of them the plane of rock cleavage has passed through the interior and removed some of the spores, but in a few this has not happened. Three of these were macerated for spore counts and the following figures were obtained (the counts being only approximate as some of the spores broke up in preparation).

Approximate Diameter of Capsule	Approximate Spore Numbers
0.6 mm.	104
0.8 mm.	336
0.9 mm.	372

These figures suggest that the number of spores is, as might be expected, roughly proportional to the capsule volume, in which case the smallest should have well under fifty and the largest perhaps a thousand.

The capsule has a very conspicuous wall, which is best seen in dehiscent fragments, but can nevertheless be made out in the intact sporangia. The wall is composed of cells of nearly uniform size, typically 50 μ wide, and the majority are square in shape. The inner surface of the cells bulges into the capsule and is highly polished: the rock nearly always splits to expose this inner surface, and not the outer, which is dull and made comparatively rough by the prominent ridges representing the margins of the cells.

As a rule there is no trace of the outer periclinal wall of the cells of the capsule wall, but in certain specimens the thick inner surface has peeled off from the rock, leaving a delicate brown film which may represent the outer surface. Also, where the plane of rock cleavage passes through a capsule so that the capsule wall is seen in section there is a suggestion of this layer (Text-fig. 20 *B*).

The wall is of uniform thickness over the whole capsule, even at its base, but there are very great differences among the capsules. In the thickest the wall cells are jet black and have often contracted from their neighbours, or have split into angular fragments in preservation (Text-fig. 20 *A*), thus making the cells appear more numerous than they are. Most often the cells are a rich chestnut brown and are uncontracted, but their substance is strong enough to retain its convexity and to allow a cell to be removed bodily with a needle. In thinner states of the wall the cells form an almost flat brown film. As these differences are seen in associated sporangia they probably represent variations in the original plant and are not the effects of preservation.

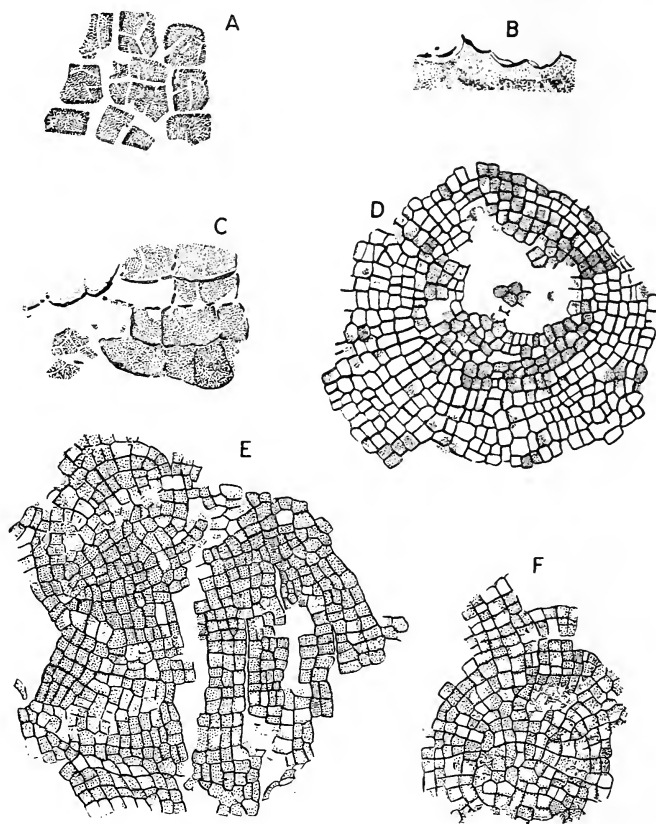
The wall cells appear to be of uniform thickness except at the margins where their somewhat greater apparent thickness may well be an optical effect. Their surface is without any of the local thickenings of ribs or spiral bands which are seen in most liverworts, nor do they show any pitting. The substance of the wall is a little less resistant to maceration than is that of the associated spores.

The wall cells have a most characteristic arrangement. They form longitudinal rows running from pole to pole of the sporangium, and transverse rows at right angles to these. These rows are by no means perfectly regular, as, indeed, would be impossible with square cells of almost uniform size covering a spherical surface, but they are nevertheless a striking feature of every specimen. Towards the poles the arrangement changes slightly (Text-fig. 20 *D-F*), the concentric or transverse rows being lost. A few sporangia show signs of another arrangement in addition to the transverse and longitudinal rows; in these there is a distinct indication of a grouping of thirty or forty cells in packets apparently formed by the subdivision of an original cell.

Among the wall fragments two sorts of sporangium ends or poles were recognised. In one, presumably the upper, end the wall forms part of a sphere; in the other the spherical surface has a considerable but not very deep depression, presumably representing the position of the foot at the base of the sporangium. On one hand-specimen the upper and lower ends lie side by side as though derived from a single sporangium.

From the great abundance of spores and wall fragments it is evident that most of the sporangia had dehisced before preservation. A few had dehisced during preservation, the spores and wall fragments being thickly scattered over a few square millimetres.

There is, however, no sign at all of any line of weakness in the sporangial wall, and the different wall fragments show no regularity apart from a tendency to be rectangular which results



TEXT-FIG. 20. *Naiadita*—sporangium wall.

A-C, the structure of the wall cells, $\times 130$. In A, the substance has contracted rather strongly, V. 4015 b. B, wall cells in section, from the edge of a sporangium, V. 4015 b. C, wall cells with less contracted substance, V. 4015 b. D-F, the arrangement of the wall cells. D, lower part of sporangial wall (the base itself is missing), V. 4015 b, $\times 45$. E, a large part of the wall of a sporangium, the apex is towards the top left corner, V. 4015 b, $\times 45$. F, apex of a sporangium. Bristol Museum, No. Ca. 7687, $\times 45$.

from the shape of the cells. This irregularity of dehiscence distinguishes the cleistocarpic type of capsule (which is also characterised by a lack of an active dehiscence mechanism), and there is little doubt that this capsule is correctly described as cleistocarpic.

The capsule contains spore tetrads only, embedded in calcareous matrix: there is no columella and no sterile cells such as elaters. Particular attention was given to this point: numerous sections were prepared (by the method of etching followed by covering with cellulose acetate and peeling off the dry film), but even in the best preparations no such structures were found. This is not perhaps conclusive because the more delicate tissues of *Naiadita* give rather unsatisfactory peels, but a most careful search through the scattered contents of the dehiscent capsules again gave negative results. The contents of other capsules were crushed and the powder mounted in oil: the two characteristic coats of the spores were conspicuous, but for the rest there was only clear transparent calcite bearing the imprint of the spore coats.

From this evidence one may conclude that the fossil capsule contains no sterile cells, and that in the original condition it contained neither thickened elaters nor a solid columella. Whether delicate sterile cells such as are seen in *Riella* and *Corsinia* were also originally absent seems less certain. The disappearance of visible cell walls in the foot of the capsule and of the spore intine illustrates the possibility that one type of cell wall may not be preserved, while a wall of different chemical nature may be preserved in fine detail. This point could perhaps be cleared up if capsules at a half-developed stage were available.

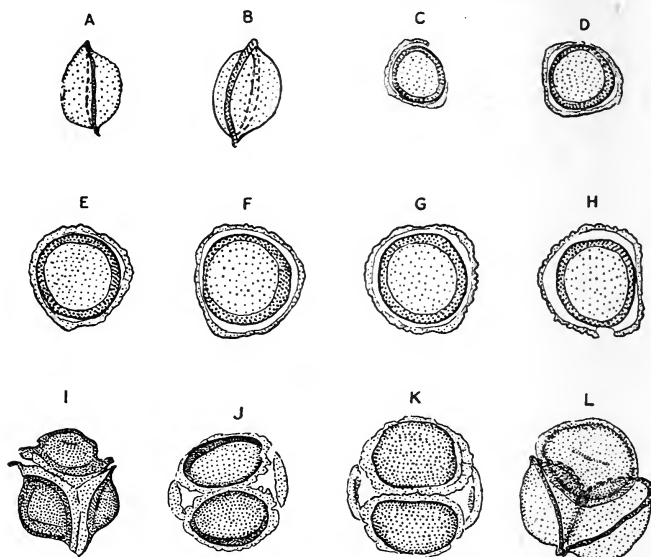
The same sort of reservation should be made for the structure of the wall: the fossil capsule definitely shows no more than one layer of wall cells; but it is possible that it might have had additional layers of delicate cells which have entirely disappeared in preservation.

Spores. The ripe spores in the sporangia and a large proportion of those scattered in the matrix are still in their tetrads, which are of the normal tetrahedral form (Text-fig. 21 I-L). Owing to the rather flat shape of the spores there is a considerable space within the tetrad which is full of calcite. The spores appear to be held together by the interlocking of the projections along their margins; in some tetrads the margins appear to fit completely, in others they leave small gaps at the corners. The tetrads occasionally survive maceration, but more commonly separate into their constituent spores; evidently they are not firmly held together. As Miss Sollas noted (1901), the spores merely need treatment with a dilute acid to free them from matrix and are then ready for close examination.

In describing the spores I have followed Leitgeb's terminology (given in Goebel 1930, p. 897). He distinguishes for an ordinary spore an inner cellulose coat or *intine* and two outer layers, the one occupying the middle of the wall being the *exine*, the outermost being the *perinium*. He also uses the term *exospore* which comprises the two outer coats. In *Naiadita* only two layers are

to be seen, and as both are cutinised I regard them as the perinium and exine, the intine being presumed to have disappeared in preservation (as it has in most fossil spores).

The spores are lens-shaped, typically $100\ \mu$ broad, $70\ \mu$ thick, but sometimes rather smaller. The wall, or at least the exine, is very hard, and many spores have been preserved with scarcely any distortion even though no calcite may have penetrated to



TEXT-FIG. 21. *Naiadita*—spore and spore tetrad.

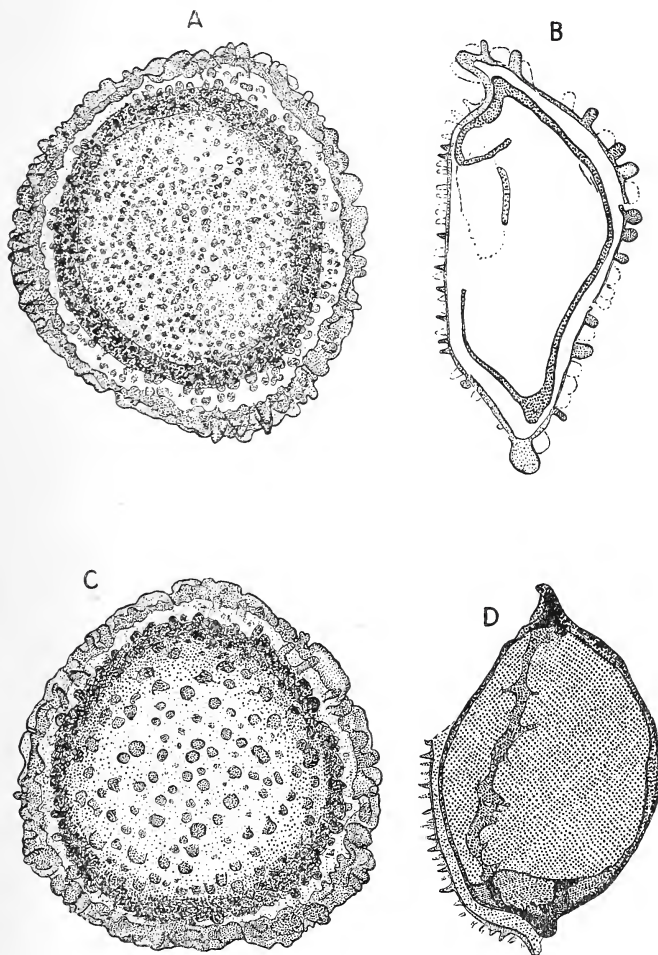
All $\times 140$.

A-H, L, isolated spores viewed by transmitted light. I-K, tetrads still embedded in rock, viewed by reflected light. A, slide V. 25312. B, slide V. 25312. C, slide V. 25311. D, slide V. 25311. E, slide V. 25310. F, slide V. 25310. G, slide V. 25310. H, slide V. 25310. I, intact tetrad; the margins of the spores appear to be completely united, V. 4015 b. J, tetrad viewed from within (by removal of part of two spores and the central matrix). Bristol Museum, No. Ca. 9279. K, tetrad viewed from outer side, V. 4015 c. In J and K there are gaps where the margins of three spores meet. L, tetrad from celloidin pull; the position of the upper spores has probably been deranged, but the two lower illustrate the attachment of the spore margins, slide V. 25309.

their interior. The majority, in fact, are full of air, which forms a glistening bubble when the specimen is mounted in oil.

The exine (inner coat in the fossil) is a smooth membrane, and appears to be about $2\ \mu$ thick, except at the margin, where it is considerably thicker. Its surface is covered with very fine and rather indistinct dots (about the size of the stippled dots in Text-fig. 22 D) and in some specimens ill-marked ridges run from the thickened margins on to the surface. No definite germ pore

was seen, though a good many spores were found with the inner or outer face irregularly broken. There is no trace of a triradiate scar, nor would it be expected in a spore of this shape.



TEXT-FIG. 22. *Naiadita*—spores.

All $\times 450$.

A, inner face of spore. *C*, outer face of another spore of the same sporangium. *A* and *C* show the perinium bearing irregular projections over its margin and papillae over the surface. This is separated by a gap from the thick-walled exine. *B*, optical section of a somewhat broken spore mounted with the margin facing upwards. The exine has been injured. *D*, broken spore mounted with the margin facing upwards. Only a small part of the inner face of the perinium is present. The thickened rim of the exine is conspicuous. All from slide V. 25310.

The perinium (outermost coat) is much thinner (of the order of 1μ thick) and is fragile. In surface view it may be nearly circular, but more commonly tends to be somewhat triangular. The margin is considerably thickened, and forms a prominent rim which is very irregularly broken up into teeth of varied form. This rim does not project in exactly the equatorial plane, but is inclined slightly inwards (continuing the curve of the outer face of the spore); a feature often shown distinctly in the intact tetrad.

Both the inner and outer faces of the perinium are ornamented with projections, but these are of distinct sorts. On the outer face (outside in the tetrad) the projections are relatively few blunt tubercles, on the inner they are more numerous sharp spines; both have in addition smaller and less definite projections. This coat has no germ spore nor triradiate scar.

The contents of the spores have not been preserved. Both the spore coats resist dilute or concentrated sulphuric acid even at boiling point, but are bleached by $\text{HNO}_3 + \text{KClO}_3$ and then, when placed in alkali, are greatly swollen or dissolved. In this they agree, in my experience, with the cuticles of a number of recent spores, but are less resistant than most fossil spores. The size and appearance of the spores only vary within narrow limits. A few sporangia have spores which are of less than the normal size (Text-fig. 21 C, D), though the structure of their spore coats is normal.

The constancy of the ornamentation of the *Naiadita* spore, its resistance and its remarkably well characterised coats, should make it an easily distinguishable zone fossil, and it might prove worth while searching for it in the equivalent of the *Naiadita* horizon in localities where this fossil is unknown from macroscopic remains.

Antheridia. The most serious gap in the account of *Naiadita* is the absence of any information about the antheridia. Repeated search was made for them both in layers containing small fragments and in layers with complete plants, and though a considerable number of possible antheridia were found these were of varied type and altogether unconvincing. The most likely were ill-preserved oval bodies the size of gemmae in or near certain of the terminal cups ("gemma cups"). These bodies, as has been remarked on p. 31, might equally well be immature gemmae or delicate-walled antheridia.

Since *Naiadita* produced plenty of archegonia, many of which were fertilised, it seems likely by analogy with recent Bryophytes that it should have produced antheridia in very large numbers. Antheridia of liverworts, however, have often far more delicate walls than the archegonia; after dehiscence their walls first swell up and then break down, while old but unfertilised archegonia

of the same age become hardened and long remain conspicuous (as in *Pellia* and many other genera). I suggest that the failure to recognise them in *Naiadita* is due to the antheridia being relatively delicate, and in part perhaps to their confusion, if preserved at all, with ill-preserved gemmae.

PREVIOUS WORK ON NAIADITA.—The early accounts of *Naiadita lanceolata* are chiefly of importance in connexion with the name, and have already been summarised on p. 16. Of the three specific names in Buckman's paper I have chosen *lanceolata*, since it is mentioned first; moreover, it was originally suggested by Brodie, and also happens to be descriptive of the commonest form.

Other contributions fall under two heads: botanical investigation of the structure of the plant, and geological records of its occurrence.

The botanical work really starts with Brodie's idea adopted by Buckman (1844, 1850) that *Naiadita* was a freshwater plant, like *Naias*: in Buckman's figures (1850) the plant looks exceedingly like a small *Potamogeton*, the cell walls being made to look like veins.

Starkie Gardner (1886, p. 203) realised the moss-like character of the leaves and stated that Brodie had sent him a moss-like capsule. He concluded that *Naiadita* was closely allied to *Fontinalis*. Unfortunately he gave very little evidence in support of his views, so that although they were nearly correct they were disregarded by later workers.

Seward (1898, p. 240) briefly discussed *Naiadita*, but left its systematic position entirely open.

In 1901 Miss I. Sollas described the vegetative structure very much more accurately than had been done before, and recognised and described the sporangia. With some of her interpretations I disagree, in particular with her conclusion that this plant is a homosporous Lycopod. This need not be discussed fully: she obviously would not have reached it had she known that the plant bore archegonia. She does not consider Starkie Gardner's nearly correct view that *Naiadita* was a Bryophyte (a moss). Some of her morphological conclusions were correct, but although others are untenable, they were not unreasonable on the evidence then available. As far as one can judge, Sollas must have studied her material in the dry state, and it happens that the fine details are not shown well unless wet, preferably with an oil. She also used a method of grinding away the rock and exposing deeper layers, though she was unable to obtain sections.

I agree with her in uniting Buckman's three species as *N. lanceolata*. This and *N. obtusa* represent comparatively narrow and broad-leaved forms respectively; even greater differences are, however, normally found between the upper and lower leaves on

a single plant. The appendages shown for *N. petiolata* are probably gemma cups and perhaps young perianths; but no specimen shows these organs to the exclusion of leaves, and I feel sure that Buckman's figure (1850, p. 415, f. 4) is a restoration, or else represents a damaged specimen.

With Sollas's general interpretation of the sporangium and spores I agree, and with her observation that the leaf was non-vascular and one cell thick. This observation, however, she attempted to explain away, suggesting, in accordance with her view that the plant was a Lycopod, that all but the upper epidermis had perished. Careful study of the epidermis of the axis at the attachment of the leaf has shown, however, that this is impossible; the tissues are complete and nothing is missing.

In her account of the stem, she says that beneath the epidermis, as the rock is ground away, smooth-walled tubes are exposed, and beneath them the epidermis on the under side. From her figure and the statement that the tubes are sometimes "frayed out at the broken ends of a stem," I conclude that these are the rhizoids, though she interpreted them as an internal stele. Such rhizoids normally form an investment of the lower part of the stem, but I cannot fully account for her statement that they are enclosed between two epidermal layers—unless the first was the epidermis or other cell layer of the stem and the next an underlying leaf. I have never seen any suggestion of an internal tube in the stem.

Sollas's statement that the sporangium was axillary is no doubt due to the conspicuous presence of a perianth leaf in her preparation; she also stated that it was sometimes terminal, probably because it was borne at the end of a little pedicel which might appear as though terminal.

Later authors (e.g., Seward, 1904) have endorsed Sollas's conclusions, though Hirmer (1927) points out certain anomalies in the facts on which they were based.

The geological literature may be summarised very simply. When *Naiadita* was recognised as marking a single definite horizon it was noted wherever it could be found (see p. 4 for references), and was called a "moss" or a "lycopod," according to the botanical view then prevailing. Descriptions of many sections have been published in which the position of the *Naiadita* horizon has been carefully noted in relation to the other fossiliferous beds: in every case it occupies the same position in the lower part of the Cotham Series, below the "Cotham Marble," and at some distance above the highest layer containing *Pteria contorta*.

Certain authors have commented on the conditions under which they imagined *Naiadita* grew and was preserved; it is remarkable how every one has supposed that it was a water plant. This is discussed more fully below.

THE HABITAT OF NAIADITA.—The *Naiadita* bed is certainly most peculiar: I have never seen material like it. It contains no ordinary land plant of its period, but an astonishing abundance of a single species, and this a very small plant. Its associates, too, are peculiar. In most non-marine plant beds the wings of insects are the commonest animals, but here it is *Darwinula* (closely similar to the shells of the little cyprids common in ponds and lakes) and the larvae of insects; more rarely fish remains occur. The associated plants are—apart from another and rather rare liverwort—merely small freshwater algae.

I have not seen any material where the mature *Naiadita* plants are preserved in the position of growth, but there is a considerable body of evidence which suggests that it grew as a submerged plant in a lake.

(1) The abundance of *Naiadita* over a wide area could be readily understood if it covered the bottom of the shallow parts of large lakes, and was preserved in sediments laid down there or in the deeper parts of the same lakes.

(2) The abundance of plants preserved in an early stage of growth is very remarkable. In every locality embryos are probably commoner than mature plants. I am, in fact, very doubtful whether any of the innumerable isolated gemmae preserved had not germinated. A simple explanation of this preponderance is that the gemmae were deposited in the living condition and that the unconsolidated and submerged sediments provided conditions where germination started, though it was not able to proceed far (perhaps not beyond the stage when the food reserves were exhausted). This state of affairs is exactly what one would expect in an aquatic liverwort producing abundant gemmae, but it would seem to require very peculiar conditions for enormous numbers of the living gemmae of a terrestrial liverwort to find their way into such a deposit.

(3) The archegonia are most exceptional in being without any "perichaetium" or system of hairs, scales, or leaves which might conserve water and so assist fertilisation. (The perianth apparently makes its appearance after the archegonium is mature.) It would be unlikely that naked archegonia near the apex of an upright land plant would ever be fertilised, but in a submerged aquatic this would offer no difficulty.

(4) The slender stem was composed of thin-walled and presumably weak parenchyma, yet it appears from the arrangement and orientation of the leaves to have grown upright. It seems to have been better suited to life under water than on land, where it would have had to support its weight.

(5) The rhizoids are remarkable in being straight and not entangled in solid particles of soil. In recent liverworts the rhizoids mould themselves around soil grains just as root-hairs do. This fact suggests that the rhizoids of *Naiadita* grew down

into soft and very fine grained material like the chalky ooze in which they were preserved.

(6) The associates of *Naiadita*—*Darwinula*, insect larvae, and the algae (*Botryococcus* and the desmid-like *Stenixys*)—are what one might expect to find in a fresh or brackish lake deposit, and are strong evidence in its favour. The bottom of a shallow lake would provide just the habitat where a little plant like *Naiadita* could flourish in the enormous numbers needed to furnish the *Naiadita* bed, and the various points of evidence together provide strong reason to suppose that *Naiadita* grew in such a submerged habitat.

SYSTEMATIC POSITION OF NAIADITA.—*Naiadita* is richly provided with features of interest in relation to the morphology and classification of Bryophytes. Were it a living plant and fully known it would without doubt occupy a distinguished position.

The following points are of systematic importance:

1. The terete, upright stem and the spiral phyllotaxis.
2. The structure of the leaf, particularly in relation to the division of the apical cell.
3. The structure of the rhizoids.
4. The form of the archegonia and their relation to the stem and leaves.
5. The general form of the sporophyte; the structure of its wall; the absence of elaters or columella within it.
6. The structure of the spores.
7. The development of the gametophyte (from the gemmae).

Naiadita does not agree with any existing Bryophyte genus or even family in all of these characters, though every one considered separately can be closely matched in an existing genus. The same is true of other characters which are of less significance—the structure of the stem, the gemmae, and the gemma cup. It follows that while *Naiadita* can be included in the Bryophyta without any doubt, its further classification is difficult and I think impossible without some considerable morphological assumptions to explain away one or another difference. With this in view the points mentioned above will now be discussed.

1. The habit of *Naiadita* is that of a typical moss, where the stems are nearly always round in section and a $\frac{3}{8}$ phyllotaxis is common. No liverwort has this phyllotaxis, though a few have round erect stems (*Riella*, Calobryaceae and upright shoots of some Acrogynaeae). Among the liverworts the nearest approach to spiral phyllotaxis is seen among the Calobryaceae and in the Acrogynaeae where there is a $\frac{1}{3}$ divergence, though in the Acrogynaeae there is a difference in that the leaves are usually of two sorts. In *Naiadita* the leaves form a single series as in a moss, and despite close search I could find no specimen where they

could reasonably be divided into two groups as "upper" and "under" leaves. As this appears to me the most significant feature of the morphology of this plant it is discussed more fully later.

2. The leaves of *Naiadita* are fundamentally those of a liverwort. In the mosses with but one or two exceptions (Goebel 1930) the apical cell is "wedge shaped" and cuts off segments from two sides; in the leaves and similar appendages (ventral scales, perianth) of the liverworts the apical cell is "flat" and cuts off segments from its base alone. The difference in development results in a difference in the arrangement of cells in the mature organ which is often well marked. Moreover, in most mosses there is a midrib and often a specialised margin, while in *Naiadita* these features are absent as in most liverwort leaves. A close approach to the leaf of *Naiadita* is found among the species of *Riella* with well-developed leaves—especially *R. clausonis* and *R. parisii*; those of the Calobryaceae are less similar, having no well-defined apex; those of the Acrogynae are usually different, having two apices. Among a very large number of leaves of *Naiadita* I found no example with two apices, the only approach being in cases where some part of the margin had grown out and given an irregular leaf. The leafy ventral scales of the Marchantiales—especially those of *Riccia natans* grown in water—and the leafy lobes of *Fossombronina*, though more different, might also be compared with the leaves of *Naiadita*.

3. The rhizoids are unicellular and thus unlike those of mosses. They are exactly of the type usual among the liverworts, except the Calobryaceae (which have none) and the Marchantiales (which have tuberculate thickenings on some rhizoids).

4. The archegonia, having a one-layered venter and being sessile (in relation to the perianth), agree with the Sphaerocarpaceae, Marchantiales, and some Jungermanniales, but differ from the type which is normal in the mosses. Unfortunately I could not determine the number of cell-tiers of the neck, which has been used as a systematic character in living liverworts. The perianth of the archegonium is very interesting: it is comparable with the ring of leaves round the archegonia of mosses and with the various types of scaly, leafy, or cup-shaped perianth in the liverworts: in *Riella*, for example, the perianth has a similar cell structure, but is tubular instead of being leafy. The morphology of the perianth is discussed later.

5. The sporophyte consists of a spherical capsule and perhaps a small hemispherical foot: there is no seta. The capsule wall is of one layer of cells and these have an evenly thickened inner wall. The capsule opened irregularly: it was thus cleistocarpic. There is no columella and no elaters.

The most similar sporophytes are found in the Marchantiaceae, for example, in *Corsinia*, which has sterile cells. Whether *Naiadita*

produced them is uncertain. Slightly less similar sporophytes are found in the Sphaerocarpaceae (which differ in having a distinct seta), though interesting points of resemblance to certain species of *Riella* may be noticed in the way the capsule tends to come off its stalk and float away intact (Cavers 1903) and in the thickening of the wall cells.

6. The spores are very characteristic and belong to one of the types found in the liverworts. Among the spores of such species as I have been able to study for comparison, the most similar are those of the South African species *Riella alatospora* Wigglesworth (1937); rather less similar spores are found in other species of *Riella* and of *Corsinia*. In all ordinary mosses, on the other hand, the spores are small and usually simple; in the cleistocarpic genera alone they are large, but differ in structure. The tendency for the spores of *Naiadita* to remain in tetrads is interesting: certain liverworts, *Sphaerocarpus* spp., *Riccia curtisii* (see Duthie & Garside, 1936) have even more firmly united tetrads and normally germinate in this position to give two male and two female plants. In *Riella* they are not united.

7. The embryo plant is not sharply marked off from the ordinary gametophyte as is the protonema of a moss, but grows directly into it, as is usual in the liverworts. It must be admitted that the embryo derived from the fairly large gemma, not the sporeling, is what is known in *Naiadita*; this is perhaps unimportant since the germination of spore and gemma in recent Bryophytes are often similar.

Other points which may be mentioned, though of less taxonomic significance, are:

8. The lack of tissue-differentiation in the stem, which consists of large-celled parenchyma. In this *Naiadita* agrees with *Riella* and a good many other liverworts: I do not know whether any mosses have this structure in their stem, but some sort of fibrous layer is, I think, normal.

9. The gemmae. Comparable multicellular gemmae are widely scattered through the Bryophytes, e.g. in certain Marchantiales and in *Metzgeria*, *Riella*, *Tetraphis* and the "bulbils" of various other mosses. In *Marchantia* and in *Tetraphis* they are produced in cup-shaped organs, though in neither are they very similar in detail to those of *Naiadita*.

From this survey it will be seen that *Naiadita* agrees in most features with the liverworts; but with the mosses in the general form of the shoot alone. I have, in fact, classified it as a Hepatic, and in this group I refer it, though tentatively, to the Sphaerocarpaceae near the Riellaceae, as being the least different and involving the least difficult assumptions.

The chief points of agreement with *Riella* are the round, upright stems (of some species of *Riella*) the form and structure of the leaves, the rhizoids, the way the archegonia are borne, the general

form of the sporophyte (particularly the wall), lack of columella or elaters, and the spores.

The differences are the absence of a thalloid lamina (which in *Riella* bears the antheridia), the radial arrangement of the leaves, the leafy (instead of tubular) perianth, and the lack of any sporophyte seta.

The lack of a minute seta such as occurs in the other Sphaerocarpaceae is not perhaps a fundamental difference, since forms with and without a distinct constricted seta are both included in one order as at present recognised—the Marchantiales. The differences in thallus seem more serious, though they are scarcely greater than exist between the genera at present placed in the Sphaerocarpaceae. This difference is examined fully later and it is shown that it is possible to regard the gametophyte and perianth structure of *Riella* as being modified from the condition obtaining in *Naiadita*.

Naiadita shows some points of agreement with certain of the Marchantiales without elaters—*Corsinia*. Here the agreement in sporophyte structure is very close, but here also the agreement ends. No liverworts are less like *Naiadita* in plant body than the Marchantiales; indeed they show nothing that can be interpreted as a real approach to a radial, leafy shoot. It is quite impossible to classify *Naiadita* here.

Naiadita may also be compared with certain Jungermanniales, particularly the Calobryaceae. This family, which includes the very similar genera *Haplomitrium* and *Calobryum*, agrees in having an upright stem with radially placed leaves; in other respects, however, the differences are very considerable: the leaves lack a pointed apex, there are no rhizoids and the sporophyte is of altogether more elaborate construction (though its one-layered wall is at least a point of agreement). Next in resemblance among the Jungermanniales are the Acrogynaeae, a few of which have almost radially symmetrical stems, though the leaves differ in possessing two growing apices, at least in the younger stages, while most of the Acrogynaeae differ still more in their dorsiventrality.

To summarise: every feature of *Naiadita* is Bryophytic, and it is certainly a Bryophyte. With somewhat less certainty I regard it as a Hepatic, and with still less certainty an ally of *Riella*, though the latter is only possible if certain morphological assumptions are accepted. Though agreeing in some points with certain Marchantiales and with the Calobryaceae of the Jungermanniales, the differences appear so great as to preclude *Naiadita* being classified in either group. Thus if not to be placed in the Sphaerocarpaceae it must stand alone.

NAIADITA AND BRYOPHYTE MORPHOLOGY.—*Naiadita* should be considered along with the other fossil Bryophytes. The number

known is fairly large, but they show very little. The Tertiary forms are apparently very like living ones, and these I will not discuss. There is a Mesozoic (mainly Jurassic) group, and a Carboniferous group.

Of the Carboniferous group the vegetative organs alone are known. A few of them look like mosses, but their fine structure is unknown (*Muscites polytrichaceus*); another is of moss structure but unknown habit (*M. bertrandi*)—see Walton 1928 for references. The liverworts are more numerous and much better known; some are thalloid (like *Aneura*), another has a lobed thallus (*Hepaticites lobatus* Walton), and one is definitely leafy—*H. kidstoni* Walton (1925, 1928). The last-named has been compared with the acrogynous liverworts by various authors, but the suggestion that it is most like *Treubia* is certainly attractive. All these liverworts can be matched, in such features as they show, by members of the Jungermanniales.

In the Mesozoic there are a good many liverworts, but not a single moss has been discovered. Again (with the exception of *Naiadita*) the vegetative organs alone are known. Nearly all consist of dichotomising thalli without a suggestion of leaves, and most specimens give no real indication of the thallus anatomy or of rhizoid structure, so that although described under such names as "*Marchantites*" they are strictly unclassifiable, and the name *Hepaticites* Walton would seem preferable. *Palaeohepatica rostafinskii* Raciborski (see Troll in Hirmer 1927, p. 141) probably has marchantiaceous air chambers. Of those whose structure and rhizoids are known *Hepaticites laevis* Harris (1931, 1937) has no trace of air chambers and has unthickened rhizoids as in the Jungermanniales, while *Hepaticites glebosus* Harris (1931), which again has unthickened rhizoids, has a lobed and waved thallus recalling the recent liverwort *Moerkia*.

The conclusion which can be drawn safely is that liverworts looking like the Jungermanniales certainly go through the Mesozoic to the Carboniferous; the Jurassic age of the Marchantiales and the Carboniferous age of the mosses is less certain. This really throws no light on Bryophyte evolution beyond indicating that they are an ancient group: we do not even find a suggestion whether they reached their climax of morphological development in the past, like so many Pteridophyte families. The other fossils, therefore, give so little help that *Naiadita* must after all be considered by itself, and it is not safe to assume because of its fairly considerable age, that it is particularly primitive.

The recent liverworts have been closely studied, and the structure of their gametophytes and reproductive organs are to a large extent known. The various genera, or rather the individual organs of these genera, provide some very striking morphological series which are commonly taken to be evolutionary series. This is not the place to review such theories, nor am I competent to

do so, but I must express my surprise as a newcomer to Bryophyte morphology at the assurance expressed by nearly all authors on Bryophyte phylogeny in dealing with what is manifestly unknown. The literature is full of the statement that one plant is "obviously more primitive" than another, and no argument is advanced even though the opposite theory is in the field. In studying phylogeny it should be obvious that morphological series may often not represent evolutionary series at all, and, even if they do, it is a matter of extreme difficulty to decide which end of such a series is primitive.

The prevailing theory, or at any rate the one most often repeated, is that the liverworts form a series showing upgrade evolution from an ideal simple "*Sphaero-Riccia*" type to the leafy gametophyte and better developed sporophyte of the Acrogynae; and then, though perhaps with less certainty, to the gametophyte and more elaborate sporophyte of the ordinary moss. This view finds full expression in the writings of Cavers (1910-11), Campbell (1918), and Schiffner (1917). These writers consider that the leafy habit arises as follows: The earliest types were leafless "thalli" (as in the diminutive kinds of *Sphaerocarpus*). These thalli developed short multicellular filaments on the ventral surface (mucilage hairs), which in the course of evolution became converted into one-layered cell-sheets or ventral scales, and these sometimes, if conditions allowed, developed chlorophyll and became under-leaves. At the same time the thallus enlarged and became divisible into a thick midrib and relatively thin "wings," and the wings were apt to grow locally to form a crisped or frilled margin. The wings then divided up into definite segments which became leaflike. The apical cell then became three-sided and the midrib a round axis: this is the condition in the Acrogynae. The final stage in the liverworts would be seen in *Calobryum* (Campbell 1920) where the upper and under leaves become almost indistinguishable, and in *Haplomitrium* where their arrangement is no longer in clearly marked rows. Transition to the moss gametophyte, though implied, is not worked out in detail owing to the absence of known intermediates, but I suppose that *Naiadita* might now be taken as such an intermediate!

The opposite view has been put forward in a general form by Wettstein (1924) alone; though on many points the views of Goebel and others are in agreement, and Verdoorn (1932) has proposed a classification on these lines. According to this view reduction has been the prevailing change in the Bryophytes; the moss gametophyte is primitive, the liverwort thallus advanced and reduced, the various intermediate types mentioned above being taken in the reverse order. As this theory of reduction has never been fully worked out, more space must be devoted to it here than to the theory of advance and elaboration.

(1) A primitive form of liverwort might be conceived as a

plant with an upright rounded stem bearing spirally arranged, flat photosynthetic ramuli or leaves, and attached by unicellular rhizoids. The apical cell would be three-sided. A slight amount of differentiation might be expected between the ordinary leaves and those associated with the reproductive organs. Since unicellular rhizoids on the stem form a feeble absorptive system, the fullest development of such a plant might be expected to occur only in a damp place or even under water. *Naiadita* agrees closely with such a postulate; so in general terms do the mosses; so also, but rather less closely, do certain seaweeds.

(2) Owing to the feeble rhizoid system, land forms of such a plant would have a strong tendency to develop a creeping habit. (Goebel, who has developed this idea, suggests that the prevailing difference of habit between the upright mosses and creeping liverworts is related to the feebler rhizoid system of the liverworts.) Such a creeping habit involves shading one side of the stem, and a tendency to dorsiventral symmetry would develop. If the stem bore leaves in three ranks with one of these on the ventral side, one would expect this set to be reduced to mere scales or to "mucilage hairs," or to be lost altogether. The leaves associated with the reproductive organs would in a land plant acquire an increased protective value, leading to considerable differentiation from the vegetative leaves.

(3) In creeping shoots in general there is always a strong tendency towards local inequalities of growth, twisting the lamina into the horizontal plane. Where the leaves are attached by a broad base as in the leafy liverworts either the incubous or the succubous modification is possible. (Both arrangements as well as the unmodified transverse arrangement are found in the Acrogynae.)

(4) A thalloid lamina might develop in various ways: for example, by a change in the position of the chief growing region of the leaves resulting in their "fusion" or adnation to form a lamina, as in *Metzgeriopsis*.

Opinions are divided as to how the various half-foliose genera such as *Fossombronia*, *Blasia*, *Treubia* should be regarded (see, for example, Cavers 1910, Goebel 1930, Buch 1930, 1932, Wijk 1928). I think that anyone who has studied the forms assumed by *Fossombronia* when cultivated in weak light or darkness would hesitate before describing this genus as possessing a mere thalloid lamina divided up into leafy lobes. Even the thalloid *Pellia* often shows distinct leaf-like lobing of its margin (though I do not know what relation this has to the segmentation of the apical cell), and *Sphaerocarpus*, which has been regarded as the ideal of a simple thallus, is very possibly a minute and vestigial liverwort (Douin 1930).

Many of the Anacrogynae may be described as completely thalloid with no trace of leafy lobing; for example, most species

of *Aneura* and *Metzgeria*. So too in the Marchantiales there is no suggestion of leafy lobing, and very little of a marginal wing: conceivably such a thallus might represent an "axis" alone; the scales on the lower side or elsewhere being the representative of leaves.

In *Riella* another type of thallus seems to have been evolved—namely, a dorsal outgrowth of the axis. No explanation of its origin is offered, but in any case the change from a radial shoot to a flat thallus would be likely to involve a change in the apical cell from three- to two-sided, such as is found in the thalloid liverworts.

There is no doubt about the existence of a series of intermediates between the more and the less leafy Jungermanniales, and it would seem that it may illustrate an evolutionary trend. The mere completeness of such a series does not, however, show the direction; any possible indications from other evidence must now be examined.

I have met nothing among the writings of the supporters of the "upgrade" theory which appears to me relevant to this important point of the direction of evolution. There are some points which appear to me significant in favour of the reduction theory, though it would not be surprising if they were shown to be meaningless.

(a) There are, I think, some grounds for believing that the leaves in the Acrogynae are fundamentally transverse in attachment. In a few genera all the leaves are strictly transverse, but in most the lateral leaves are very oblique, being tilted either so as to overlap or be overlapped by the next leaf in front. Both types of obliquity arise largely as a result of inequality of growth of the stem tissue; in some genera they are strictly transverse in origin; in others, where the whole formation of the stem apex is oblique, they may be distinctly oblique in origin (Buch 1930), but much less so than the mature foliage. Many examples, moreover, are known where the reproductive shoots, which are more erect than the vegetative, are also more radial in organisation, and so too are etiolated shoots and the starved-looking shoots of young plants. In such shoots not only are the lateral leaves less oblique than usual, but there is less difference than usual between the lateral and the ventral leaves.

If these plants stood alone or if a similar set of facts were adduced for a group of higher plants, I feel that no one would hesitate to regard the dorsiventrality of the shoot as secondary, and probably evolved in relation to the one-sided lighting of the creeping shoot.

(b) The most radial living liverworts—the Calobryales—seem to me to fit most easily into the reduction view. This group has been described in two ways. For *Calobryum*, which has leaves in three ranks, Goebel (1890) and Buch (1930) take the almost

radial stems to be fundamentally radial, with occasional slight dorsiventrality caused by unequal lighting, while Campbell (1918, 1920) takes the stem to be fundamentally dorsiventral, with a difference between lateral and ventral leaves that is important and indeed fundamental but often hard to see. In *Haplomitrium* accounts again differ from the extreme views of Stephani (1900), who thought he could distinguish a sterile ventral row of leaves from two lateral sets with axillary antheridia (a statement which later investigators have shown to be incorrect) and Gottsche (1843), who simply described the arrangement of leaves as irregular in the upper part. Some specimens of *Haplomitrium* which Mr. W. E. Nicholson lent me for examination agree in the lower part of their leafy stems with Müller's account (1907): the leaves are definitely in a $\frac{1}{3}$ spiral which is sometimes unmodified, sometimes a little modified by a twisting of the axis shown by the direction of the epidermal cells. In the upper part the leaves were altogether irregular in size and in attachment: that is to say, I could recognise no underlying principle. For example, one finds first a group of small leaves arising at almost the same level, then a few large ones in a loose spiral, then a few of unequal size nearly vertically above one another, and so on. In these specimens the axis, as can be seen from its surface cells, is untwisted or only shows negligible torsion.

While either view is possible, I think it safe to say that anyone who looks at good figures or specimens of the Calobryales, without letting himself be influenced by opinions formed from the study of other genera, will agree that Goebel's view, that these plants are organised on a radially symmetrical plan, would be the natural one to form for this group. If the Calobryales stood entirely alone their radial organisation would not have been called in question, any more than it is in a flowering plant or moss shoot with $\frac{1}{3}$ phyllotaxy.

(c) *Naiadita* appears to me to fit in best with the reduction views. It may be conceded that it can be fitted in to either view, but while on the "reduction" theory it can be simply accepted for what it appears to be, on the "elaboration" theory it would have to be regarded as a most misleading plant in which the leaves, though of two fundamental sorts, and the shoot, with fundamental dorsiventrality, give no indications of their nature. The case is really just the same as in the Calobryales, but with a plant that appears even more radial.

Whether such arguments as these three are cogent enough to cause anyone to form an opinion on the relative value of the two theories I doubt: to me the matter appears open, though I prefer the reduction view as being simpler. Church (1919) has set forth various reasons for regarding the radial type of organisation in general as the primitive, and many of his arguments would appear to apply as well to Bryophytes as to seaweeds.

Naiadita may also afford evidence on the question of the morphological nature of the archegonial perianth. This consists of about four organs which are just like foliage leaves. They arise from the archegonial axis at short intervals, not in a true whorl, though as development proceeds they appear to form a whorl. On this subject, too, there has been some controversy, the views being (1) that the perianth (in, e.g., the Acrogynaeae) can be regarded as composed of leaf units (Knapp 1930) and (2) that the perianth is often so different from leaves that such a view is meaningless or wrong. *Naiadita* occupies an extreme position; the perianth is more like a number of leaves than in any other liverwort, and it is natural to describe it as consisting of leaves. This provides material for the supporters of the leaf theory, though no one would say that all liverwort perianths need be of the same nature.

On other matters *Naiadita* appears to me to provide no evidence. Its sporophyte is remarkable, but whether or not it has sterile cells it is not unique and can be matched by that of some living genus.

The investigation of a plant like *Naiadita* can chiefly throw light on organ-evolution. Phylogeny is obviously a far more obscure matter which can scarcely be contemplated until the history of all the important organs is clear. As this history is still dark, it would be altogether wrong to suggest, for example, that because *Naiadita* combines features found in certain genera belonging to different families that it should be regarded as a common ancestor.

SUMMARY.—The Rhaetic plant *Naiadita lanceolata* Buckman is given an emended diagnosis (p. 18), and the stem, leaf, rhizoids, gemma cup, gemmae, embryo, archegonia, perianth, sporophyte, and spores are described. *Naiadita* is considered to be a submerged water liverwort, and is tentatively referred to the family Riellaceae of the Sphaerocarpales. Its most exceptional features are its radial organisation and the leaflike form of the perianth. The bearing of these features on liverwort morphology is doubtful, but it may be considered either as an extremely primitive or an extremely advanced plant in the organisation of its gametophyte, according to the view taken of the Bryophytes as a whole. I regard it as primitive.

- V. 3357. Two specimens. Stems, leaves, etc., **a**, type specimen, said to be figured Buckman 1850, p. 414, fig. 2. **b**, said to be figured, *ibid.*, fig. 3 (see p. 19). "*Estheria* Bed, Nr. Bristol." *P. B. Brodie Coll.*, 1895.
- V. 3356. Two counterparts. Stems, leaves, etc. Figured Buckman, 1850, p. 415, fig. 4 (composite figure). "*Estheria* Bed, Nr. Bristol." *P. B. Brodie Coll.*, 1895.
- V. 4015. This group of specimens includes the best examples of *Naiadita* shoots and other organs.

Block a. Shoots, gemma cups, sporangia, etc. Shoots (Text-figs. 4, 7 C); perianth—destroyed in preparation (Text-fig. 17). Also catalogued under *Botryococcus*.

Block b. Very numerous sporangia, some bearing a perianth, some isolated; also many fragments of the wall and isolated spores. Small stems, leaves, archegonium and perianths. Sporangium (Pl. I, fig. 1, Text-fig. 18 G); sporangium wall (Text-fig. 20 A-E); spores (Text-fig. 21 I); leaf (Text-fig. 10 A); archegonium (Text-fig. 16 D).

Block c. Fine shoots, etc. Gemma cup (Pl. I, fig. 3; Pl. II, figs. 1, 2; Text-fig. 14 A); perianth (Text-fig. 16 E); shoots (Text-fig. 6); leaf (Text-figs. 8 A, 9 D); spore tetrad (Text-fig. 21 K). Also catalogued under *Hepaticites*.

Block d. Many fine shoots. Two halves of sporangial wall in association, lower half (Pl. V, fig. 1).

Block e. Stems, leaves, etc., described and figured by Seward, 1904, p. 16, pl. ii, figs. 2, 3.

There are seven other blocks.

Nr. Redland, Bristol. *W. H. Wickes Coll.*, 1900.

- V. 11010. This group of specimens includes some well-preserved examples of *Naiadita* sporophytes.

Block a. Good leafy shoots; a sporangium and perianth with a pedicel possibly attached but more probably preserved in contact with a leafy shoot. Fruiting perianth (Text-fig. 18 C).

Block b. Good leafy shoots, gemma cups, sporangium with perianth; a young stage of perianth formation. Perianth (Pl. IV, figs. 3, 4; Text-fig. 18 B, E, F, H).

Block c. Leaves, gemmae, embryos (Text-figs. 9 C, 11 G). Also catalogued under *Hepaticites*.

Block d. Leaf (Text-fig. 9 B).

Block e. One leafy shoot is over 2 cm. long.

Block f. Shoot apex with ill-preserved organs of doubtful nature (gemmae or antheridia?). The block includes a layer with fish bones and also a sun-cracked layer.

Block g. Shoots with gemma cups, perianths and archegonia. The block includes layers of fish bones.

Block h. Gemma in a gemma cup.

New Clifton, Bristol. *W. McPherson Coll.*, 1903.

- V. 24809. Leaves and gemmae. Leaf (Text-fig. 8 B). Also catalogued under *Botryococcus* and *Hepaticites*. Pen Park Road, Southmead, Bristol. *G. A. Kellaway Coll.*, 1936.

- V. 24810. (a) Well-preserved shoots, gemmae, embryos, archegonia, Rhizoids (Pl. I, fig. 4; Pl. IV, fig. 1); stem (Text-fig. 7 E); gemmae (Pl. II, fig. 4; Pl. IV, fig. 2; Text-figs. 11 H, 12 B, C); leaf (Pl. V, fig. 3, Text-figs. 8 C, 9 A, 10 F); archegonium (Text-fig. 15 B). (b) Archegonium (Pl. III, figs. 1-4; Text-fig. 15 A). (Also catalogued under *Stenixys*.) Pen Park Road, Southmead, Bristol. *G. A. Kellaway Coll.*, 1936.

- V. 24812. Well-preserved leafy shoots; also an incomplete, empty perianth? with three very unequal leaves, gemma cups, and "compound eye of insect." Gemma cup (Text-figs. 13 G, J, 14 B). Also catalogued under Branched Filaments. Redland, Bristol. *G. A. Kellaway Coll.*, 1936.

The following specimens (V. 25270-V. 25286) are all from Henleaze Road, Bristol. *G. A. Kellaway and T. M. Harris Coll.*, 1937.

- V. 25270. Fragments. An abnormal sickle-shaped leaf; archegonia; a gemma cup (Text-fig. 14 D). Fish remains on back.
V. 25271. Fragments. Leaf (Text-fig. 9 G).
V. 25272. Fragments. Leaf (Text-fig. 9 E, F).

- V. 25273. Fragments. Gemma and embryos (Text-fig. 12 *A*).
 V. 25274. Fragments. Gemma (Text-fig. 11 *I*).
 V. 25275. Fragments. Abnormal leaf (Text-fig. 10 *E*).
 V. 25276. Fragments. Gemma (Text-fig. 11 *F*).
 V. 25277. Fragments. Abnormal leaf (Text-fig. 10 *D*). Gemmae; body segment of insect larva.
 V. 25278. Fragments. (Pl. I, fig. 2); abnormal leaf (Text-fig. 10 *B*).
 V. 25279. Fragments. Gemma and embryo (Text-fig. 12 *D*); body segment of larva.
 V. 25280. Good shoots, sporangia, perianths, gemma cups, archegonium. Gemma cup (Text-fig. 13 *D*).
 V. 25281. Good shoots, archegonia, gemma cups. Gemma cup (Text-fig. 13 *B*); stem with rhizoids (Text-fig. 7 *A, B*).
 V. 25282. Fragments. Longest leaf seen (over 6 mm.), gemmae. Abnormal leaf (Text-fig. 10 *C*).
 V. 25283. Gemma cup (Text-fig. 14 *E*).
 V. 25284. Fragments. Gemma (Text-fig. 11 *F*).
 V. 25285. Gemma cups, archegonia, etc. Gemma cup (Text-fig. 14 *C*); connected body segments of insect.
 V. 25286. Fragments. Archegonium (Text-fig. 15 *C*).
 V. 1437. Two small specimens bearing stems, leaves, etc. One is labelled "*N. lanceolata*," the other "*N. obtusa*." "Rhaetic, Bristol." *P. B. Brodie Coll.*, 1886.
 V. 3394. Large specimen. Rather poorly preserved shoots; a shoot bearing archegonia, possibly with enlarged venters. An accompanying label in Brodie's handwriting states that "these freshwater plants . . . are not monocotyledonous but Cryptogams, an aquatic fluviatile moss allied to recent *Fontinalis*, according to J. S. Gardner and others," and that they were "discovered in 1844." Also three fragments with similar specimens. Taunton Road, near Bristol. *P. B. Brodie Coll.*, 1895.
 V. 3397. Two fragments. The larger bears some poor specimens of *Naiadita* shoots, the smaller only rhizoids and fragments of an animal, perhaps an insect. The specimens bear an inscription in ink, "Moss allied to *Fontinalis*." (Also catalogued under *Botryococcus*.) Wainlode Cliff, Gloucester. *P. B. Brodie Coll.*, 1895.
 V. 13169. Two large specimens, counterparts; both show many well-preserved shoots, gemma cups, etc., and in addition both *Darwinula* sp. and *Estheria minuta* var. *brodieana* in the same bedding plane as the plants. The larger shows the remains of a small animal, perhaps the head and jaws of an insect larva. New Clifton section, Redland, Nr. Bristol. *L. Richardson Coll.*, 1914.
 V. 13170. Poorly preserved isolated leaves, stem fragments, etc. Noticed Richardson 1903, p. 148. (Also catalogued under *Botryococcus*.) Coombe Hill, Cheltenham, Gloucester. *L. Richardson Coll.*, 1914.
 V. 13171. Isolated leaves, a spore. Noticed Richardson 1903, p. 137. Wainlode Cliff, Gloucester. *L. Richardson Coll.*, 1914.
 V. 13172. Poorly preserved leaf and stem fragments. Noticed Richardson 1903, p. 168. (Also catalogued under *Botryococcus*.) Highgrove, Minsterworth, Gloucester. *L. Richardson Coll.*, 1914.
 V. 13173. Poorly preserved leaves and a great many slender threads, possibly comparable with filamentous algae, but not definite enough for description. Noticed Richardson 1903, p. 152. Bourne Bank, Nr. Defford, Worcester. *L. Richardson Coll.*, 1914.
 V. 13174. Well-preserved isolated leaves, fragments of other organs. Fragments of a small animal, possibly insect jaws. Fine threads (cf. filamentous algae). On a slightly different bedding plane are *Estheria* shells, a fragment of a moderate-sized lamellibranch and

other animals. Noticed Richardson 1903, p. 164. (Also catalogued under *Botryococcus*.) Garden Cliff, Westbury-on-Severn, Gloucester. *L. Richardson Coll.*, 1914.

- V. 13175. Poorly preserved leaves and other fragments, small fossil regarded as body segment of an insect larva. Noticed Richardson 1911, p. 65. (Also catalogued under *Botryococcus*.) Hapsford Mills, The Vallis, Nr. Frome, Somerset. *L. Richardson Coll.*, 1914.
- V. 24811. Leaf fragments. (Also catalogued under *Botryococcus* and Branched Filaments.) Uphill Road cutting, Nr. Weston-super-Mare, Somerset. *G. A. Kellaway Coll.*, 1936.
- V. 25291. An isolated archegonium. (Also catalogued under *Hepaticites*.) Henleaze Rd., Bristol. *Kellaway and Harris Coll.*, 1937.

The following slides (V. 25309-V. 25315) were prepared from material from Redland, Bristol. The "sections" are celloidin peels and were prepared from V. 4015b.

- V. 25309. Very imperfect section showing some intact spore tetrads (Text-fig. 21 L).
- V. 25310. Spores, the contents of one sporangium (Text-figs. 21, E-H, 22.)
- V. 25311. Section through sporangium; the spores are rather small (Text-fig. 21 C, D).
- V. 25312. Section through sporangium; spores in lateral view (Text-fig. 21 A, B).
- V. 25313-14. Sections through sporangia.
- V. 25315. Wall of dehiscent sporangium in surface view.
- In. 27082. [In the Fossil Insect Collection.] Good stems and gemma cups. Also several specimens of *Hepaticites solenotus* q.v. (p. 70). Also on one side the body of a large insect labelled as "pupa case of dragon fly," and on back, in same bedding plane as *Naiadita*, a shell of *Chlamys valoniensis* Defranc. Coldharbour Farm, Redland, Bristol. *W. H. Wickes Coll.*, 1928.

Collection of the Geological Survey and Museum:

- PM. 877. Three specimens similar to V. 4015 in the British Museum Coll. Block A. Good stems, sporangia, gemma cups, etc.; impression of base of sporangium. Gemma and gemma cup (Pl. II, fig. 3); gemma cup (Text-figs. 13 E, H). Block B. Similar material. Block C. Similar material: Gemma cups (Text-figs. 13 A, F). Also catalogued under *Hepaticites* and Branched Filaments. Redland, Bristol. *Presented by W. H. Wickes*.
- PM. 882. Eight fragments mounted on a card. The specimens show moderately preserved leaves and stem fragments. (Also catalogued under *Stenixys* and *Hepaticites*.) Bedminster, Bristol.
56513. Well-preserved fragments of leaves, sporangia, etc. There are a good many associated specimens of *Darwinula*, two shells of *Estheria* and a number of problematical ? animal fossils of the same kinds as at Henleaze. This locality is interesting because it shows "suncracked" layers, but according to Kellaway there are no interbedded layers with remains of marine fish. Evidently therefore the marine layers though a frequent component of the *Naiadita* bed are not invariable. (Also catalogued under *Botryococcus* and *Stenixys*.) Crox Bottom, Novers, Bristol. *Presented by G. A. Kellaway*, 1937.
56516. Limestone with numerous shells of *Estheria* and a few very poor fragments of *Naiadita*. Harbury Cutting, Warwickshire.
56517. Fragments of various organs of *Naiadita*. Cracombe, Worcester.
56518. Fragments of *Naiadita* associated with many shells of *Estheria minuta*. Park, north of Upton-on-Severn, Worcester

Collection of the Bristol Municipal Museum and Art Gallery:

- C. 4558. Isolated leaves. Pylle Hill, Bristol. *Presented by E. Wilson.*
- Ca. 7686. Fairly good shoots with archegonia, fragments of sporangia, two fairly good specimens of "compound eye of insect." Coldharbour Farm, Redland, Bristol.
- Ca. 7687. Good shoots with gemma cups, etc. Gemma cup (Text-fig. 13 C); sporangium wall—on back of specimen—(Text-fig. 20 F); perianth (Text-fig. 16 B). Coldharbour Farm, Redland, Bristol.
- Ca. 9277. Shoots and leaves of *Naiadita*. Scale of *Lepidotus*; other smaller fish scales. The bedding plane is strongly curved. (Also catalogued under *Hepaticites*.) Coldharbour Farm, Redland, Bristol.
- Ca. 9278. Many excellent shoots with gemma cups and archegonia; sporangia with and without perianths. Perianth (Text fig. 18 A). Specimens of "insect compound eyes." Coldharbour Farm, Redland, Bristol. *Presented by W. H. Wickes.*
- Ca. 9279. Three blocks. All show excellent leafy stems and gemma cups. (a) Sporangia on back, spores (Text-fig. 21 J). (b) Gemma cup (Text-fig. 13 I). Many fish scales. (c) Shoot with gemma cup and perianths (Text figs. 16 A, C). (Also catalogued under *Hepaticites*.) Coldharbour Farm, Redland, Bristol. *Presented by W. H. Wickes.*
- Cb. 1538. Moderately preserved shoots and gemma cups. The specimen bears two specimens of the body of a fairly large insect and on the back is labelled "Nymph case of Dragon fly." Redland, Bristol. *Presented by W. H. Wickes.*
- Cb. 2660. Leafy shoots, a fish scale on a different plane from the *Naiadita* shoots. Southmead Laundry, Westbury, Bristol. *Presented by W. H. Wickes, 1924.*
- Cb. 2661. Leafy shoots, a rather small *Estheria* shell associated with the shoots. Southmead Laundry, Westbury, Bristol. *Presented by W. H. Wickes, 1924.*
- Cb. 2662. Shoots with gemma cups, archegonia, etc.; a poorly preserved specimen of "insect's compound eye." Southmead Laundry, Westbury, Bristol. *Presented by W. H. Wickes, 1924.*
- Cb. 2663. Shoots, etc.; a well-preserved attached sporangium (Text-figs. 18 D, 19). Also catalogued under *Botryococcus* and Branched Filaments. Southmead Laundry, Westbury, Bristol. *Presented by W. H. Wickes, 1924.*
- Cb. 2664. Isolated leaves and stems. Coldharbour Farm, Redland, Bristol. It is unusual for the material to be so broken up from this locality. *Presented by Rev. H. H. Winwood, 1921.*

Reading University Collection (in the Museum of the Department of Geology):

3842. Good stems with rhizoids, etc. Redland, Nr. Clifton, Bristol. *L. Richardson Coll.*
3843. Sporangia. Redland, Nr. Clifton, Bristol. *L. Richardson Coll.*
3844. Good leafy stems. Redland, Nr. Clifton, Bristol. *L. Richardson Coll.*
3845. Good leafy stems, etc. Stem with archegonium and perianth (Text-fig. 5); stem and leaves (Text-fig. 7 D). Redland, Nr. Clifton, Bristol. *L. Richardson Coll.*

Genus **HEPATICITES** Walton 1925, p. 565.

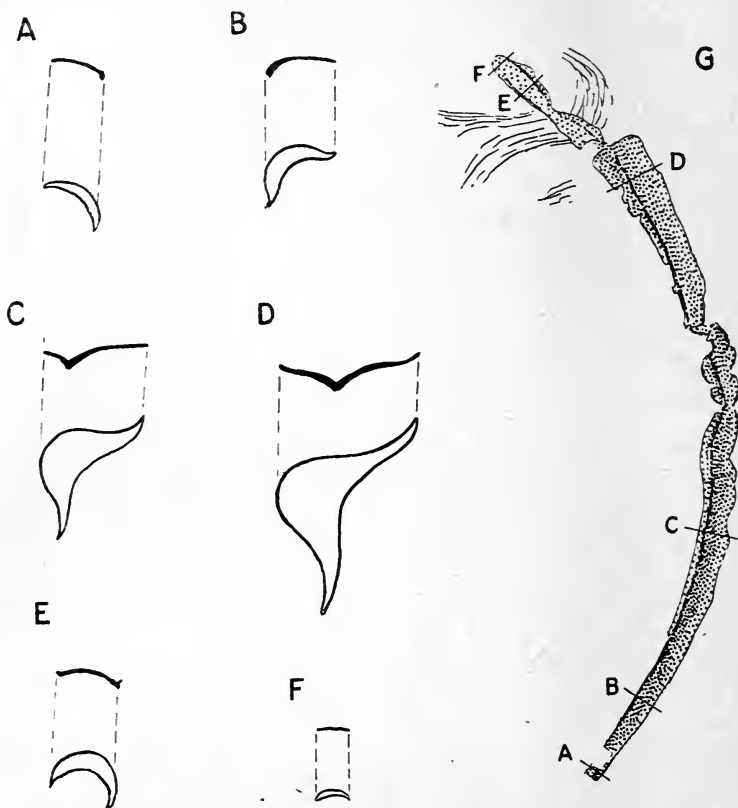
Hepaticites solenotus sp. nov.

(Text-figs. 23–25)

1937 *Hepaticites solenotus* (*nomen nudum*) Harris in Kellaway, p. 226.

DIAGNOSIS.—Thallus sparingly branched, upper surface deeply channelled, lower surface very convex. Middle region thicker

than margins, but no defined midrib present. Lower surface bearing unicellular rhizoids $25\text{--}30\ \mu$ in diameter. Margins of thallus unistratose, middle region several cells thick, cells uniform, air chambers absent.



TEXT-FIG. 23. *Hepaticites solenotus*.

To the right is a drawing of the Holotype. Geol. Surv. & Mus., No. PM. 877.
× 4.

The letters *A*–*F* mark the position of imaginary sections (based on the surface features). In the sections the upper, black drawing represents the contour and thickness of material of the specimen; the lower outline is a restoration of the presumed form and orientation of the thallus at this point. Sections × 12.

Young plants (? gemmae) circular or oval multicellular discs $450\ \mu$ in diameter or larger.

HORIZON.—*Naiadita* bed, Upper Rhaetic.

LOCALITIES.—Bristol district.

HOLOTYPE.—PM. 877c, in Geological Survey and Museum (Text-fig. 23).

DESCRIPTION.—*H. solenotus* is easy to recognise. When immersed in oil it is a light orange-brown colour quite different from the other fossils of this bed. It is rather rare, except apparently in one bedding plane at Redland, where it seems common.

In thickness it varies a good deal; when delicate (as in the margins of most specimens) it only forms a brown stain from which the overlying rock does not cleave away readily, and it is in consequence often difficult to make out the exact form of the margins, which when clearly shown are either straight or slightly and irregularly lobed. When thick, however, it forms a firm, smooth layer which can be detached in fragments from the matrix. It proves to be moderately resistant to chemical treatment: it is only darkened, not disintegrated, by concentrated H_2SO_4 at $100^\circ\text{C}.$; and only rather slowly acted on by $\text{HNO}_3 + \text{KClO}_3$, though when oxidised (bleached) it is disintegrated by dilute alkali. In its resistance it is intermediate between the ordinary cell walls and the spores of *Naiadita*.

The cell structure is seldom clear except in the thinner portions of favourable specimens, and even then the cells are far less clearly marked than in *Naiadita*. In one specimen they average 60μ long and 40μ broad. Although individual cells can scarcely be made out in the thicker regions the appearance suggests that in the middle they are elongated in the longitudinal direction, while towards the margin they are elongated in an oblique direction and form oblique rows making an angle of 30° – 40° with the margin itself.

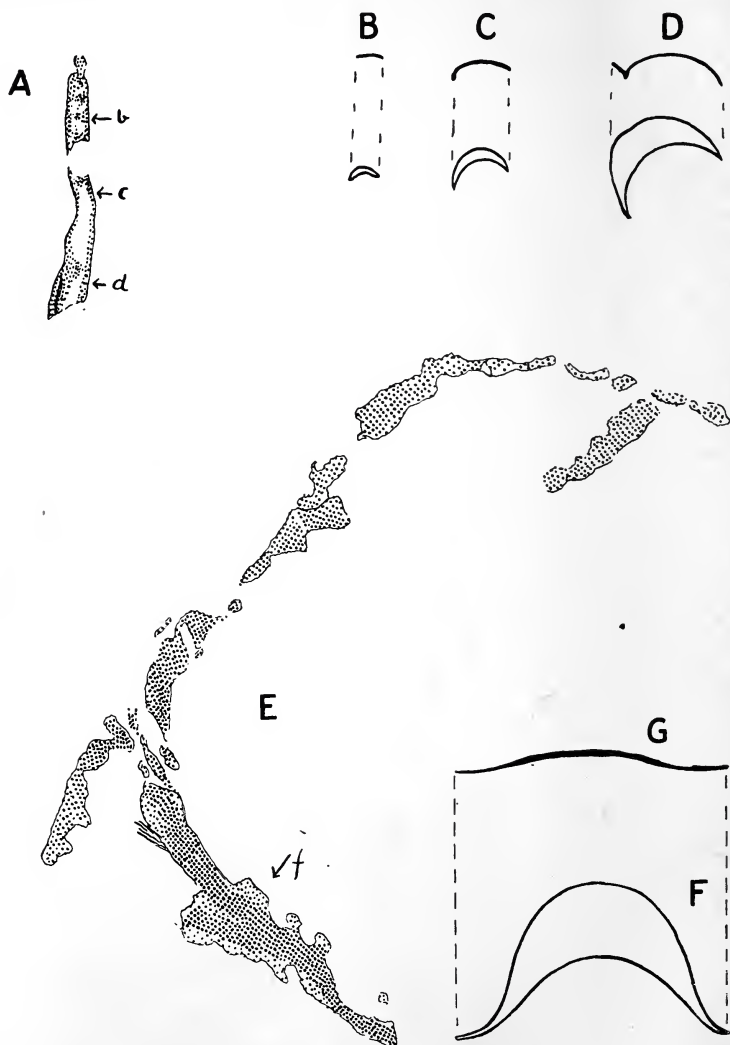
The rhizoids are only shown by a few specimens, but their structure is uniform (Text-fig. 25 G). They are narrower and a good deal more delicate in substance than the rhizoids of *Naiadita*. The various specimens suggest, or are at least consistent with the view, that they spring from the underside near the middle line.

Branching of the thallus is rather rare, and is not shown in any of the best preserved specimens. The largest specimen (Text-fig. 24 E) certainly appears to branch, but is not wholly convincing because the preservation is poor; moreover, this bedding plane is strewn with fragments, so that it is possible that the various pieces represented may not really belong together.

The apex is shown in two specimens at least; the thallus tapers and becomes more delicate and flatter towards the obtusely pointed apex.

The most remarkable feature of these plants is the variation of their surface contour. Some are strongly arched (or hollowed) as the one in Text-fig. 24 A; others have a conspicuous gutter-like furrow at some point usually well away from the middle (Text-fig. 23), others consist of two halves folded together like the covers of a book. The specimens with the strong furrow might suggest

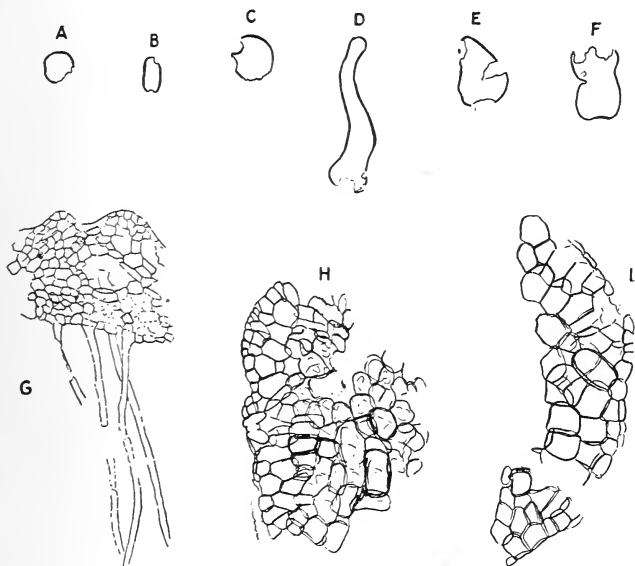
an excentric midrib; the others give no suggestion of any definite thickening.



TEXT-FIG. 24. *Hepaticites solenotus*.

A, thallus. Geol. Surv. & Mus., No. PM. 882, $\times 4$. The letters *b*, *c*, *d*, mark the position of imaginary sections, *B*, *C*, *D* (see Text-fig. 23). *E*, thallus. Bristol Museum. No. Ca. 9277, $\times 4$. (The rock is crowded with ill-preserved fragments, and it is therefore doubtful whether this figure represents a single branched specimen.) A section is shown at the position *f*. *F*, restored section. *G*, imaginary section through the specimen shown in *E* at the level *f*.

These variants can be accounted for without difficulty on the lines of Walton's theory of the manner in which a solid plant organ is changed, as the result of fossilisation, into a "compression." According to Walton (1936) when a highly compressible plant organ is embedded in a less compressible porous matrix (e.g., mud) the contour of the fossil produced depends largely on the form of the surface which happens to face downwards when it was buried. A fleshy thallus with a concave upper surface (half-moon-shaped section) may lie any way up and may happen



TEXT-FIG. 25. *Hepaticites solenotus*.

A-F, outline drawings of 'gemmae,' $\times 15$. A, V. 25287. B, V. 25288. C, V. 25287. D, V. 25290. E, V. 25289. F, V. 25290. G, part of thallus showing origin of rhizoids, V. 25293, $\times 45$. H, part of 'gemma' (margin to the left), V. 25291, $\times 80$. I, part of 'gemma' (margin to the right), V. 25292, $\times 75$.

to be twisted. With the help of this simple theory the hypothetical deformation of a body of half-moon-shaped section can be worked out for all different ways of compression. The specimens are found to agree very well with one or another of these theoretical forms (Text-figs. 23, 24).

Gemmae. In addition to the thalli just described, there are some minute specimens which I regard as gemmae. These are round or oval discs of rather varied size, but typically $450\ \mu$ in diameter. They are multicellular, two or perhaps three cells thick in the middle, but only one cell thick towards the margins, where also

the size of the cells decreases. Certain specimens, showing the gemma type of structure continued in one direction into a slender thallus, might possibly represent germinated gemmae.

The evidence for referring these organs to *H. solenotus* is (1) their marked association with the thallus, (2) their very close agreement in cell structure and particularly in the reddish colour of the wall, which is characteristic of this species alone in this flora.

Affinities. *H. solenotus* may be grouped with the other fossil thalloid liverworts, none of which is really classifiable. It is excluded from the Marchantiales by the absence of air chambers and tuberculate rhizoids, but might belong to any of the remaining families of thalloid liverworts. Among modern forms the thallus recalls that of *Aneura incurvata* (Lindb.) Steph. though the gemmae are different.

- V. 25287. Three small bodies, regarded as gemmae (Text-fig. 25 A, C).
 V. 25288. Three small 'gemmae' (Text-fig. 25 B), a portion of a thallus bearing rhizoids.
 V. 25289. A rather large 'gemma' (Text-fig. 25 E).
 V. 25290. Two specimens of 'gemmae.' Germinated 'gemmae' (Text-fig. 25 D, F).
 V. 25291. 'Gemma' showing cells rather clearly (Text-fig. 25 H). Also catalogued under *Naiadita*.
 V. 25292. Part of a 'gemma' showing cells (Text-fig. 25 I).
 V. 25293. Well-preserved fragment of thallus showing rhizoids (Text-fig. 25 G).
 The above specimens (V. 25287-V. 25293) are all from Henleaze Road, Bristol. *Kellaway and Harris Coll.*, 1937.
 V. 4015. Block c. A rather ill-preserved piece of the thallus. (Also catalogued under *Naiadita*.) Redland, New Clifton, Bristol. *W. H. Wickes Coll.*, 1900.
 V. 11010. Block c. Two small, closely associated pieces of the thallus. (Also catalogued under *Naiadita*.) New Clifton, Bristol. *W. McPherson Coll.*, 1903.
 V. 24809. Small ill-preserved fragment of thallus. (Also catalogued under *Botryococcus* and *Naiadita*.) Pen Park Road, Southmead, Bristol. *G. A. Kellaway Coll.*, 1936.
 In. 27082. [Fossil Insect Collection—on one side is the body of a dragon-fly nymph.] Several typical unbranched specimens, some showing a channelled surface and some showing numerous attached rhizoids. (Also catalogued under *Naiadita*.) Coldharbour Farm, Redland, Bristol. *W. H. Wickes Coll.*, 1928.

Collection of the Geological Survey and Museum:

- PM. 877. Block C. Type specimen. An unusually long, unbranched thallus showing rhizoids (Text-fig. 23). Also catalogued under *Naiadita* and Branched Filaments. Bedminster, Bristol.
 PM. 882. A rather narrow apical piece of the thallus (Text-fig. 24 A-D).

Collection of Bristol Municipal Museum and Art Gallery:

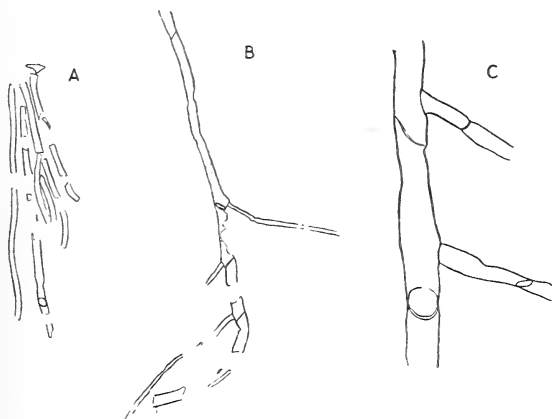
- Ca. 9277. Block bearing a very large number of indifferently preserved fragments (Text-figs. 24 E-G). Also catalogued under *Naiadita*. Coldharbour Farm, Redland, Bristol. *Presented by W. H. Wickes*.

Ca. 9279c. Ill-preserved unbranched piece of thallus. (Also catalogued under *Naiadita*.) Coldharbour Farm, Redland, Bristol. Presented by W. H. Wickes.

BRANCHED FILAMENTS RESEMBLING MOSS RHIZOIDS.

(Text-fig. 26)

The specimens described here are fragments of slender filaments which are divided by oblique septa and occasionally give rise to finer primary or still finer secondary branches. The main branches are typically $35\ \mu$ thick, which is barely half the thickness of the



TEXT-FIG. 26. "Moss rhizoids."

A, group of rhizoids, V. 25296, $\times 45$. B, lower part of a long, branched rhizoid, V. 25294, $\times 45$. C, part of a rhizoid, showing the septa, V. 25295, $\times 120$.

rhizoids of *Naiadita*. A peculiar feature shown by certain specimens is that the main rhizoid or its branches may grow somewhat thicker distally. The substance is rather darker and much more coherent than that of the *Naiadita* rhizoid.

No specimen shows a complete or attached rhizoid, but in two cases a number seem to spring from a common point.

The oblique septa and the production of slender lateral branches are the features in which these specimens agree perfectly with moss rhizoids and differ from any known filamentous algae. Many, or even most, recent mosses have rhizoids of this type and it is therefore useless to describe them under a name.

HORIZON.—*Naiadita* bed, Upper Rhaetic.

LOCALITY.—Bristol district; Uphill, near Weston-super-Mare.

SPECIMENS.—No attempt has been made to give a complete list of specimens bearing these or similar filamentous organs.

Prolonged search reveals a few on nearly every specimen, except from Pylle Hill, Bristol, where they are rare or absent.

- V. 25294. Branched rhizoid (Text-fig. 26 B).
 V. 25295. Branched rhizoids (Text-fig. 26 C).
 V. 25296. Group of rhizoids converging to a point (Text-fig. 26 A).
 The above specimens (V. 25294-6) are all from Henleaze Road, Bristol. *G. A. Kellaway and T. M. Harris Coll.*, 1937.
 V. 24811. Typical specimens. (Also catalogued under *Botryococcus* and *Naiadita*.) Uphill Road cutting, Weston-super-Mare. *G. A. Kellaway Coll.*, 1936.
 V. 24812. Typical specimens. (Also catalogued under *Naiadita*.) Redland, New Clifton, Bristol. *G. A. Kellaway Coll.*, 1936.

Collection of the Geological Survey and Museum:

- PM. 877. Block A. Specimens showing several rhizoids radiating from a point. (Also catalogued under *Naiadita* and *Hepaticites*.) Bedminster, Bristol.

Collection of the Bristol Municipal Museum and Art Gallery:

- Cb. 2663. A typical fragment. (Also catalogued under *Botryococcus* and *Naiadita*.) Southmead Laundry, Westbury, Bristol. *Presented by W. H. Wickes*, 1924.

SECTION II.—THE FLORA OF THE RHAETIC APART FROM THE *NAIADITA* HORIZON.

It has been stated before that the remaining flora is poor; it is in fact poorer than was supposed to be the case since, as pointed out below, about half the species thought to be Rhaetic are Lower Liassic.

Equisetaceous stem casts.

- V. 20537. Three poorly preserved stem casts of a *Neocalamites* or an *Equisetites* with woody bundles. The matrix is fine sandstone; the horizon is not stated. Lane House, Feckenham, Worcester. *T. J. Slatter Coll.*, 1896.

Lignite.

- V. 13165. Rather unpromising material, but this is the only plant known from the British Lower Rhaetic. Rhaetic Bone Bed, Railway cutting, Charlton Mackrell, Nr. Somerton, Somerset. *L. Richardson Coll.*, 1914.

Otozamites cf. *obtusus* (L. & H.).

- V. 10316. Impression of the top half of a typical *Otozamites* leaf. The outline of the pinnae is shown, but no leaf substance is present and the venation is not clear, so that although the specimen is very like typical *O. obtusus* (a well-known Liassic species—see Seward 1904), it cannot be determined with certainty. The bed from which it was obtained belongs, according to Richardson, to the very top of the Rhaetic, others who place the Liasso-Rhaetic boundary lower would therefore include this bed in the Liassic. Sun Bed, Quarry above Ludlow Quarry, Radstock, Somerset. *J. W. Tutchter Coll.*, 1904.

? *Otozamites* sp.

- V. 13167. An oval impression in sandstone which might well be an *Otozamites* leaflet. Noticed Richardson 1905, p. 403. The Cross, St. Hilary, Glamorgan. *L. Richardson Coll.*, 1914.

Seeds.

- V. 13166. Sandstone with casts of various sorts of seeds. Rhaetic Sandstone. The Cross, St. Hilary, Nr. Cowbridge, Glamorgan. *L. Richardson Coll.*, 1914.

Problematicum.

- V. 13168. A small and obscure fossil recorded by Richardson (1905) as "? alga." It consists of an impression filled with fine grit. The impression represents rods, 0.6 mm. wide at the base, tapering to 0.2 mm. near the tips. The rods branch and anastomose forming a net with oval meshes 1-2 mm. long. The ultimate branches are perhaps free. I express no opinion about the nature of this specimen. Noticed Richardson 1905, table facing p. 392. From the "White Lias" (part of Upper Rhaetic). Lavernock Point, Nr. Cardiff. *L. Richardson Coll.*, 1914.

SECTION III.—LIASSIC FOSSILS FORMERLY CLASSED AS RHAETIC

In that part of the "Catalogue of the Jurassic Flora" which deals with the Rhaetic (Seward 1904), specimens of *Equisetites muensteri*, *Clathropteris*, and a few other fossils are described. All these specimens are probably Lower Liassic, not Rhaetic at all. Their original labels give the age as Lower Liassic, and on a later label the age "Rhaetic" has been substituted; in consequence they were previously catalogued as Rhaetic. Most of them are stated to have been found in the "Insect Limestones" of Binton and Strensham, Warwickshire, famous localities for Liassic insects, and they are preserved in a typical Liassic matrix.

There was formerly some confusion between Rhaetic and Liassic, as certain authors classed the whole Rhaetic series as Liassic, but for a long time there has been general agreement about everything but the exact position of the boundary. The reason why the specimens were referred back to the Rhaetic is not clear; possibly it was imagined that the plants indicated a Rhaetic age. This is not, however, the case. It should perhaps be pointed out that the "Insect Limestone" from which these Liassic specimens were obtained is not the same as the "Insect Limestone" which occurs locally in the Cotham series of the Upper Rhaetic.

These Liassic specimens will only be considered in so far as they have been actually described as Rhaetic by other authors.

The following specimen is not a plant:

- V. 3359.—See Seward 1904, p. 20, where it is called ? *Araucarites* sp. This specimen has some resemblance to a fir-cone, but on detailed examination proves to be composed of non-cellular chitinous material and is undoubtedly of animal nature, though so broken up as to be probably useless. Binton, Warwickshire. *P. B. Brodie Coll.*, 1895.

The following three specimens may also very possibly be of animal origin:

- V. 3401. Specimen called "*Hippurites*" by Buckman (1850, p. 415, text-fig. 7) and ? *Cycadolepis* by Seward (1904, p. 21). Strensham, Worcester. *P. B. Brodie Coll.*, 1895.
- V. 3400. Specimen called "*Carpolithes*" by Seward (1904, p. 19, text-fig. 1) and compared by him with *Samaropsis zignoana* Nath. Binton, Warwickshire. *P. B. Brodie Coll.*, 1895.
- V. 3586. Specimen called "Ericaceous leaf" by Buckman (1850, p. 417, text-fig. 9); stated to be indeterminable by Seward (1904, p. 21). Forthampton, Gloucester. *P. B. Brodie Coll.*, 1895.
- V. 3358. Specimen called *Equisetum brodiei* (of which it is the type and only specimen) by Buckman (1850, p. 414, text-fig. 1) and *Equisetites muensteri* by Seward (1904, p. 13, pl. i, fig. 4). The specimen appears to me larger and longer in its internodes than typical specimens of *E. muensteri*, and, moreover, the leaf-teeth as figured by Seward are of different shape. I am therefore doubtful if it is rightly determined as *E. muensteri*. Two specimens of the marine Liassic crustacean *Coleia* are associated with it. Strensham, Worcester. *P. B. Brodie Coll.*, 1895.
- V. 3399. *Clathropteris meniscoides* Brongn. Figured Seward 1904, p. 18, pl. iii, fig. 2. A worn fragment but no doubt rightly named. This species is equally common in the Rhaetic and Lower Lias of other lands. "Liassic, Bristol"—no precise horizon or locality given. *P. B. Brodie Coll.*, 1895.
- V. 3585. Specimen referred doubtfully to Umbelliferae by Buckman (1850, p. 416, text-fig. 8); referred to as umbelliferous by later authors; regarded as indeterminable by Seward (1904, p. 21). The specimen is quite indeterminable. Apperley, Gloucester. *P. B. Brodie Coll.*, 1895.

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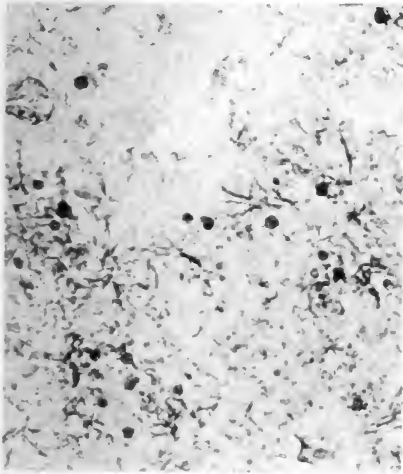
EXPLANATION OF PLATES



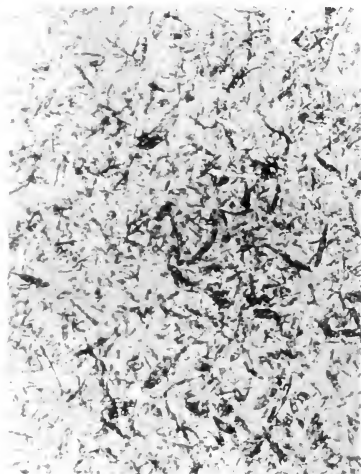
PLATE I

Naiadita lanceolata Buckman

- Fig. 1. Example of rock specimen showing fairly numerous intact sporangia, $\times 2$. **V. 4015 b**, Redlands, Bristol.
- Fig. 2. Example of rock specimen showing very numerous isolated leaves and other fragments, $\times 2$. **V. 25278**, Henleaze, Bristol.
- Fig. 3. Example of rock specimen showing numerous more or less intact shoots, $\times 2$. **V. 4015 c**, Redlands, Bristol.
- Fig. 4. Base of a plant showing rhizoids, $\times 12$. **V. 24810 a**.



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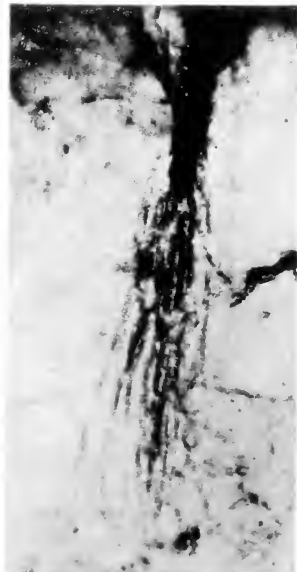


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NAIADITA.





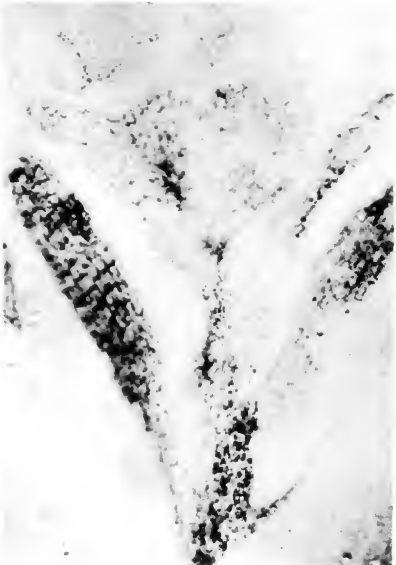
PLATE II

Naiadita lanceolata Buckman

- Fig. 1. "Gemma cup" containing small masses of tissue of doubtful nature, $\times 23$. V. 4015 c, Redlands, Bristol.
- Fig. 2. "Gemma cup" containing a dark body of doubtful nature, $\times 23$. V. 4015 c, Redlands, Bristol. This cup is also figured in Text-fig. 14 A. Both this and the specimen shown in Fig. 1 are figured at a much lower magnification on Pl. I, Fig. 3.
- Fig. 3. "Gemma cup" with part of the wall dissected away to show a gemma apparently attached to its base, $\times 25$. Geol. Surv. & Mus., No. PM. 877 A.
- Fig. 4. Gemma and embryo plant (also shown in Text-fig. 12 C), $\times 32$. V. 24810 a.



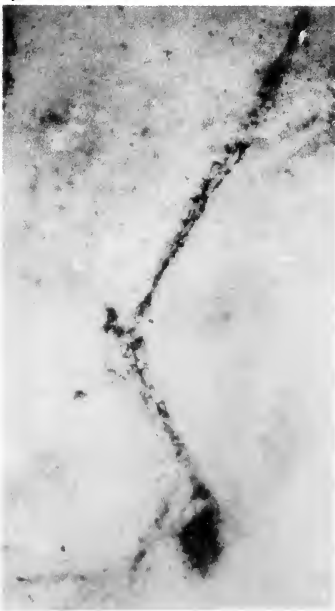
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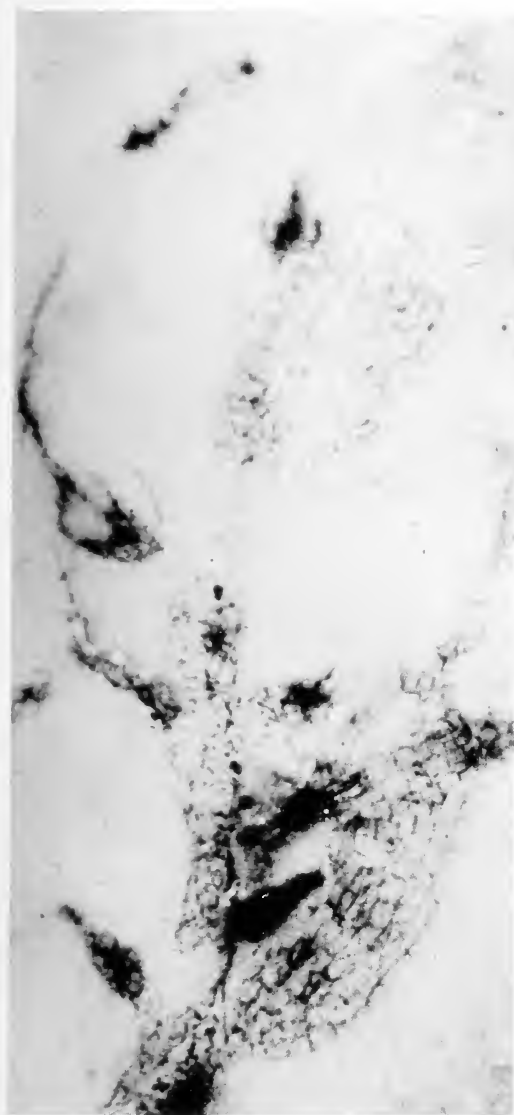




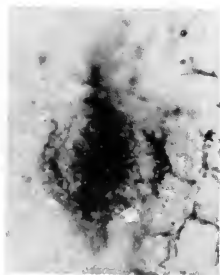
PLATE III

Naiadita lanceolata Buckman

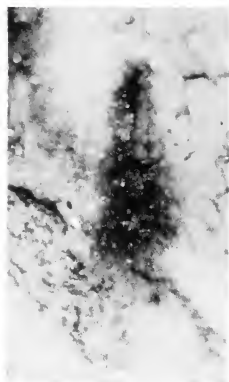
- Fig. 1. Shoot bearing a number of archegonia (some of which are out of focus owing to the unevenness of the rock). V. 24810 b, $\times 56$.
- Fig. 2. Uppermost archegonium (neck out of focus). It has a definite though small perianth; a leaf lies underneath and to its right, $\times 112$.
- Fig. 3. Archegonium (dark specimen near base on right of Fig. 1). There is no perianth, $\times 112$.
- Fig. 4. Archegonium (bottom of Fig. 1). The neck is out of focus, there is no perianth, $\times 112$. This specimen is also figured in Text-fig. 15 A.



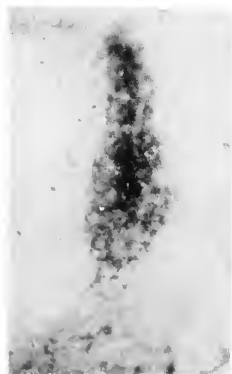
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NAIADITA.





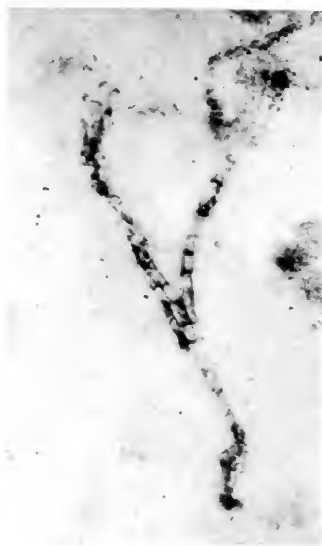
PLATE IV

Naiadita lanceolata Buckman

- Fig. 1. Rhizoids (attached to base of a leafy stem). V. 24810 a, $\times 50$.
Fig. 2. Gemma and young plant. V. 24810 a, $\times 32$. (Also shown in Text-fig. 12 B).
Figs. 3 and 4. Pedicel bearing four perianth leaves and enclosing part of the wall (the apex) of the sporangium. Fig. 3 at higher plane of focus showing a perianth leaf on the left, Fig. 4 at a lower plane showing the sporangium wall, other perianth leaves and the hollowed-out top of the pedicel. V. 11010 b, $\times 25$. The specimen is also shown in Text-fig. 18 F.

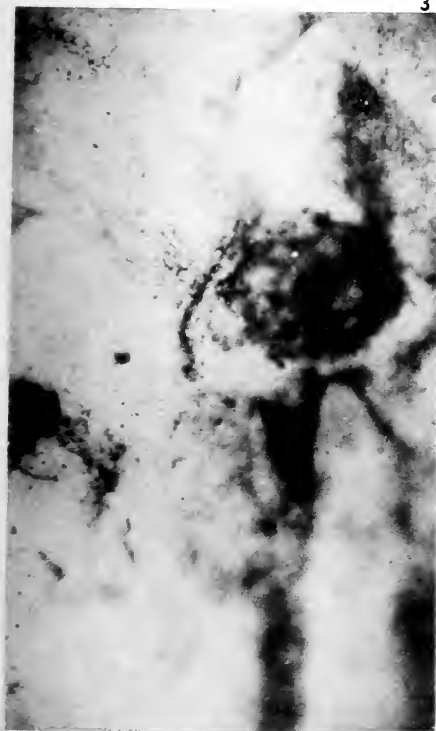


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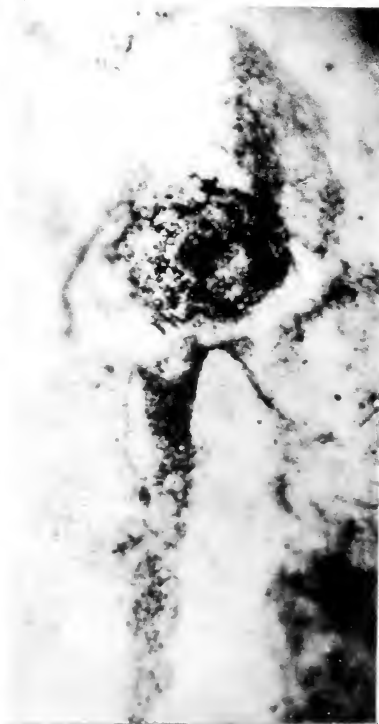


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NAIADITA.



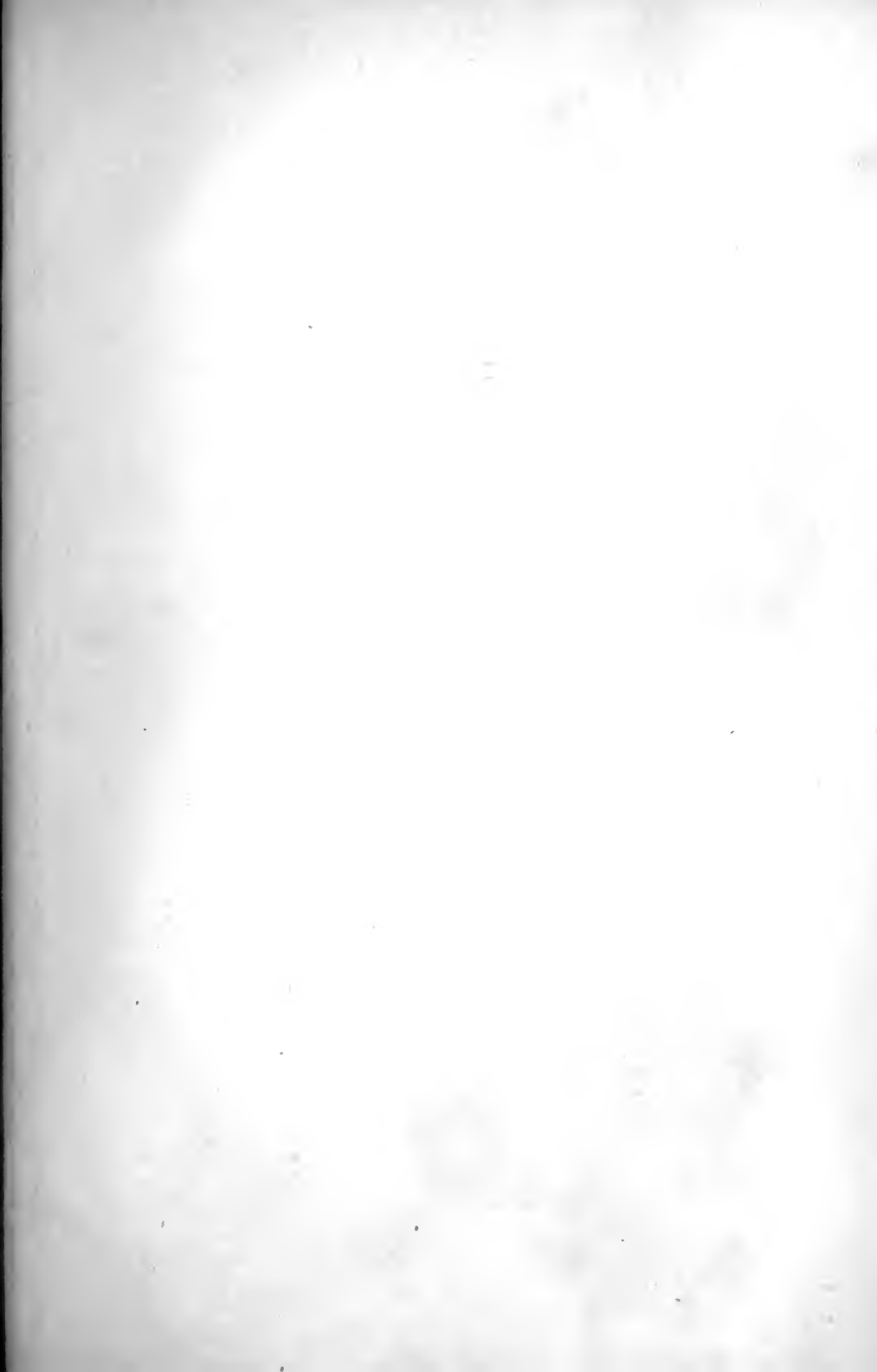


PLATE V

Naiadita lanceolata Buckman

- Fig. 1. Impression of part of the wall of the sporangium—the base. The specimen as a whole is concave, but there is a raised ring round the middle. The relief has been heightened by covering the specimen with sublimed NH_4Cl . V. 4015 d, $\times 72$.
- Fig. 2. Shoot bearing remains of three archegonia, all of which are surrounded by fairly advanced perianths. The lower specimen on the left is also shown in Text-fig. 16 G, V. 4015 c, $\times 23$.
- Fig. 3. Typical leaf apex. The lower part is obscured by another leaf. V. 24810 a, $\times 70$.

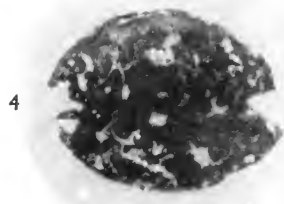
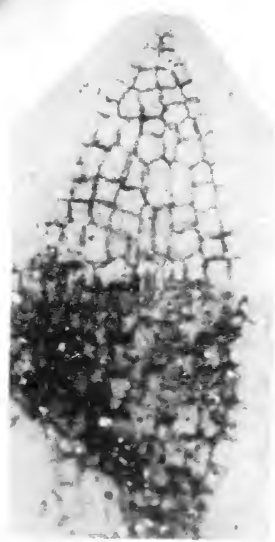
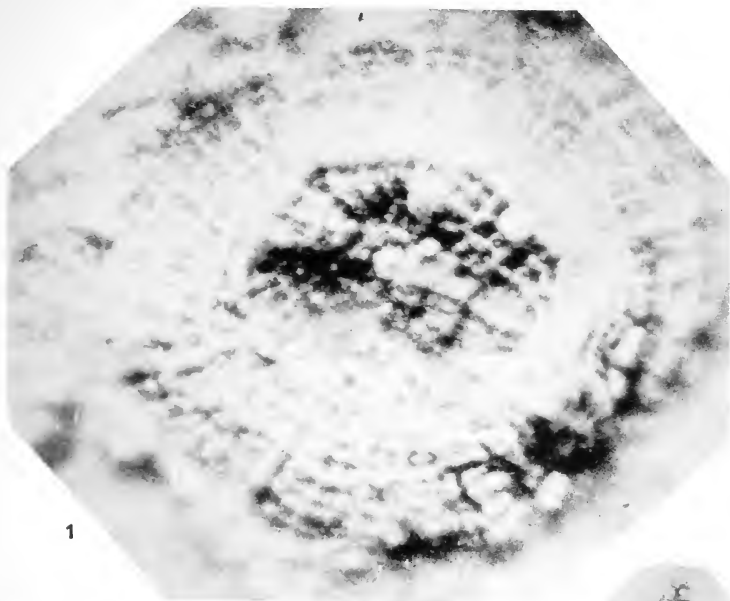
Stenixys cosmarioides sp. n.

- Fig. 4. Specimen photographed under xylol. The wall substance has contracted and cracked and some of it has peeled off, but shows no sign of pitting. V. 24810 a, $\times 100$.



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